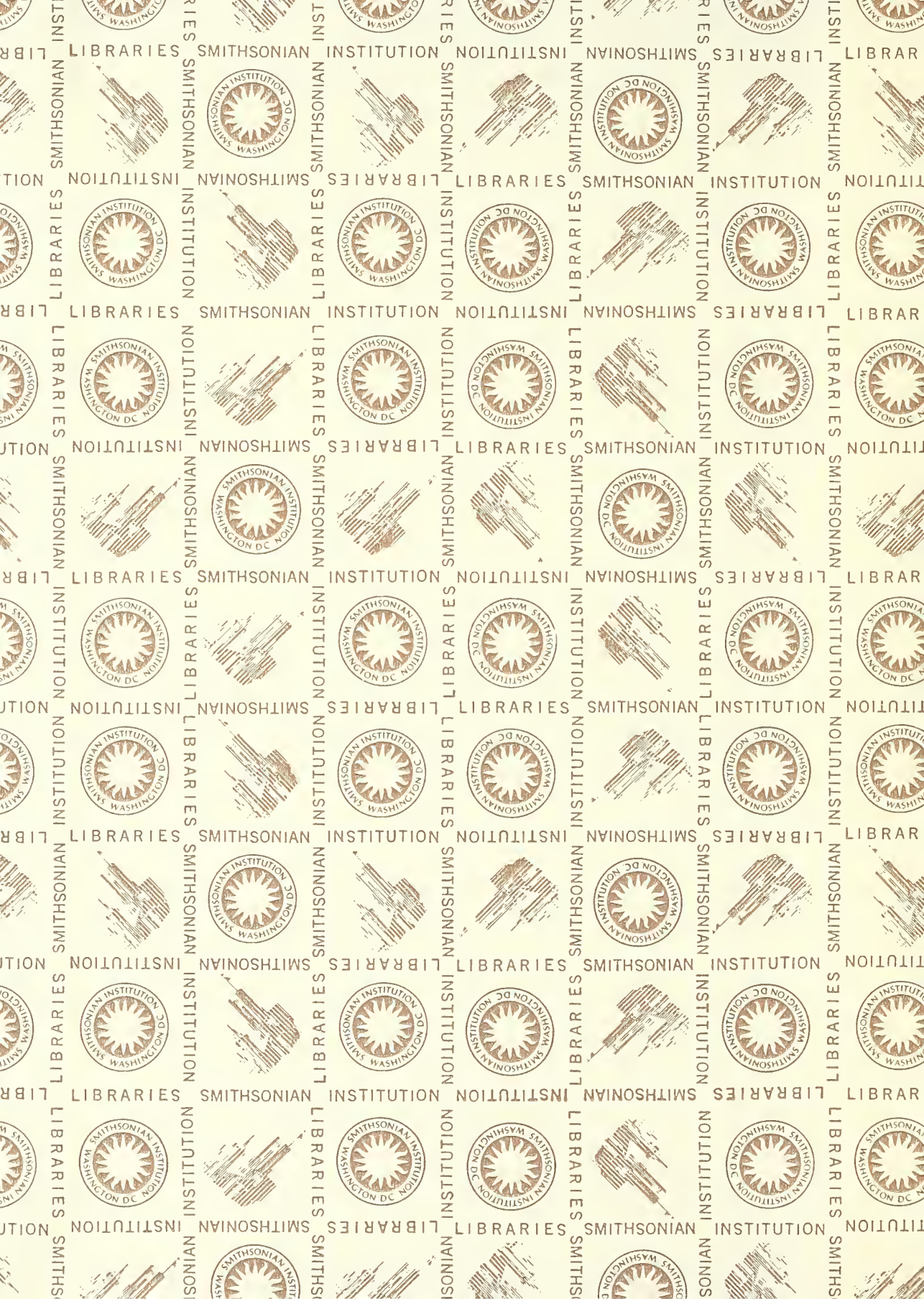






F. M. Hueber

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THE FOSSIL CYCADS

by TOM M. HARRIS

Fourth Annual Address, delivered 8 March 1961

ABSTRACT. The fossils considered are those in which attribution of one organ to the Cycadales (in the strict sense) is supported by the evidence from a different organ believed to be of the same plant. It thus deals with *Palaeocycas*+*Bjuria*; *Androstrobus prisma*+*Pseudoclenis lanei*; *Androstrobus* spp.+*Beania* spp.+*Nilssonia* spp. Two classic fossil Cycads, *Cycadospadix* and *Dioonitocarpidium*, are considered not fully convincing. The kind of evidence needed is mentioned and the need is urged for assembling separate fossil organs into further synthetic plants.

THE Recent Cycads are a small family of Gymnospermous seed plants, scattered through the tropics of the world and of no particular economic importance but very familiar to botanists. Many of them look like squat palms. The 'fossil cycads' are a large and very indefinite assemblage of all sorts of plant organs, but nearly all of them of Mesozoic age. To some authors they comprise about a hundred genera and a few thousand species, in fact almost everything ever called a fossil cycad, irrespective of present views. Many are rather more discriminating than this and, in this address, I shall limit myself extremely to those fossils which not only have every appearance of being truly Cycadean but in which this appearance is strongly supported by a second line of evidence.

Botanists agree that the Cycads ought to be found fossil. All their organs, stem, leaf, male and female organs are large, robust, and strongly characterized and as it seems well suited to be preserved and then to be recognized. And we have long been impressed by their archaic features; one such is fertilization by spermatozoids, but there are half a dozen others and they look as though they had persisted without change from very early times. Cycads are so archaic that had they been extinct and only known fossil, it would have been a very easy thing to point a moral. And so when a century or more ago leaves just like modern Cycad leaves were found in vast numbers in the Mesozoic rocks, and also a fair number of similar stems, and even a few suitable reproductive organs, everybody gladly recognized them as Cycadean and some people even called the Mesozoic the Age of Cycads. The literature was filled with generic names recalling those of Cycads. Gradually, however, this simple picture became complicated and confused. Certain plants called fossil Cycads and with very suitable looking stems and leaves proved to have totally different reproductive organs, and for these another class, the Bennettitales, was established. We now think that a good deal more than half of the fossils, formerly called Mesozoic Cycads, belong to the Bennettitales but the proportion is uncertain. A few have been proved to have Bennettitalean reproductive organs; a much larger number are linked with these few by some special character, for instance, the epidermal structure of the leaf. Others in which the structure is unknown are just vaguely associated. On the other hand, a minute number of fossil Cycads have been proved to be Cycadean in the strict sense (the ones considered here) and a moderate number are associated with them on more or less impressive evidence. A very considerable number of the fossils originally proposed as fossil Cycads are still uninvestigated and of unknown affinity.

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It is partly conservatism which makes some of us continue to call the Bennettitales fossil Cycads even though we do not think they have anything to do with them, but partly a reaction to imperfect knowledge. We have the small group of the definite fossil Cycads, the moderate-sized group of definite Bennettitales, and associated with each is a large penumbra of less and less clearly attached fossils. We use our terms today in such various ways that we must cause real confusion. There are all varieties of opinion between those who regard the Bennettitales as so remote that they may as well be called unrelated (this is my position) and those who, while recognizing that they are quite different in some organs, feel that other organs are so similar that they must be related through a not very distant common ancestor. A term has been created which I find repugnant, but it is generally used and I freely admit it has its usefulness; this is Cycadophyte. It was intended to cover Recent and fossil true Cycads, the fossil Bennettitales and fossils not yet clearly placed in either family. It has been found a conveniently broad filingspace to accommodate several other Mesozoic genera. Some of these like *Caytonia* and *Pentoxylon* are rather fully known and they will not fit well into any plant class. Of course, when they are pushed in here, they broaden the Cycadophytes still further and, as far as I can see, the fossil Cycadophyte is just a short name for any Mesozoic plant with a leaf constructed on a more or less pinnate plan, without regard to the other organs of the same plant! The trouble with such a word is that people *will* regard it as a natural class and proceed from that to make mistakes.

In the early days it was inevitable that isolated plant organs alone were considered, and those that looked Cycadean were considered Cycadean. It was when the plants began to be put together that it became plain that the whole plant would not fit fully into the Cycad mould. This directs our attention to one of the main differences in outlook between fossil botanists with botanical outlook and plant morphologists working on modern plants. With modern plants you may consider a particular organ or even just a small part of it, but you never forget that it belongs to a certain whole plant. With fossils you take what you have, that is some isolated organs, and you engage in thoughts about them without having any whole plant at all, though you may create one as a hypothesis. This sort of thought has always fascinated the fossil botanist and no doubt always will, but it is very dangerous and I think he could have used his mind to better advantage. As I shall emphasize at the end of the address, botanical progress depends on working towards a whole plant.

THE CASE OF *PALAEOCYCAS*

The first fossil Cycad I shall accept on my restricted definition is *Palaeocycas integer*, described by Florin in 1933. It is not a complete plant but it has two important organs, the foliage leaf called *Bjonia simplex* and the seed-bearing organ or megasporophyll to which the name *P. integer* properly applies. In fact both organs had been described fifty years earlier from the Rhaetic of Sweden and Florin was revising old specimens, but if you compare the first treatment with the second you will see the second is over twenty times longer and possibly twenty times as laborious. This gives one reason why such work is rare. Florin gives a spirited reconstruction of *Palaeocycas*; it consists of two known fossils synthesized on the basis of the recent genus *Cycas*: it is perfectly clear what is fact and what surmise. Florin could, had he wished, have used a different model; for instance the tropical Ginger family, which happens to have leaves looking very like those

of *Palaeocycas*, could provide several alternative models, though they might be less attractive botanically since we believe these fossils are unrelated to the Gingers.

There is another difficulty. Not one of the specimens of megasporophyll figured still bears its seeds. It is true that the stalk shows bulges which look as though they were the points where large seeds were borne, and I can only say that if I had been studying the specimen, I would have assumed that it did bear seeds in the way Florin showed. But until seeds are seen, let us always remember that this is an assumption.

Accepting then that the organ is a seed-bearing megasporophyll, what is the evidence that this and the leaf, which has been described under an entirely different name, belong to the same plant? And then when we have the evidence that they are correctly put together, what is the evidence that the whole plant is a Cycad?

The organs are found separately and most of the specimens are broken. The evidence for attributing them to one species is only circumstantial; no specimen suggests continuity. There is, in the first place, the evidence of association. The fossils are preserved in a deltaic deposit full of fossil plants and in such a deposit association of fossil organs shows that they were produced at the same time and in nearly the same place. It is the more suggestive because the leaf is an uncommon fossil, having only two Swedish localities and the megasporophyll is rare, occurring in one of the leaf localities. Reproductive organs in general are so much rarer than leaves that when in a flora preserved near where it grew, you find several specimens of a reproductive organ, you have a right to expect to find the appropriate leaf with them. Still there are many other species of leaves also associated.

Then there is the evidence of agreement in structure. The only part of which we have information is the cuticle of the epidermis, but this is excellently preserved and open to study at high magnification. By numerous preliminary studies, Florin showed, as others had done less systematically, that certain features of the epidermis tend to run through all the organs of a plant. This is specially true of the stoma. We may add that when a part happens to be green and rather leaf-like, it often has rather close resemblance to the cuticle of the leaf. The cuticle can have family characters running through all the organs and it can also have specific characters which act even if obscurely as a specific label for the various organs.

Florin showed that there was extremely close agreement between the leaf cuticle and that of the expanded lamina of the megasporophyll. There are also points of agreement between the stalks of the two organs. He examined all the associated leaves of other species and found that all of them differed more or less; so there is no rival leaf to claim the megasporophyll. We will take it that the two organs of *Palaeocycas* are rightly attributed to one plant (though always bearing in mind that there is an element of risk in this assumption); what then is the evidence that it is a true Cycad? In fact there is no living Cycad with a leaf just like the fossil but the essential architecture is similar so the difference is not too disturbing. The structure of the stomata is exactly similar and somewhat special to this family, so the leaf fits well enough. The megasporophyll is more like that of *Cycas* than anything else known to us on earth (but again we bear in mind the reservation that it has not yet been proved to bear *Cycas*-like seeds).

What has happened is that instead of the knowledge of two separate bits of fossil plants, we have the much more impressive coherent knowledge of the pair, with certain reservations it is true but not ones that I would let worry me. What should we now do?

Plainly we need more; we should look for further circumstantial evidence bearing on the question whether the two organs belong together; for instance, we might search the second leaf bearing locality for associated megasporophylls. And then there are great gaps in our botanical knowledge. It is probably too much to hope that we could find the real stem so as to replace Florin's hypothesis by fact; and too much to hope that, if we do find it, we might learn how the leaves and megasporophylls were borne in relation to one another. There is a better hope that with further collecting we might find megasporophylls still bearing seeds and that such specimens might reveal a good deal of their seed structure as it has done in another fossil Cycad. It is not too much to hope that we might find the pollen-bearing organs.

The mine which yielded *Palaeocycas* has long been closed, so the only hope is that it is eventually found in another locality. Florin's material was collected nearly a century ago by men who may have been acute and discriminating and the work of such men is not to be despised; but it really is a matter of luck if they found and preserved the precise kind of specimen which was needed to make progress in the laboratory a century later.

If such progress were made, what result would we expect? Probably the circumstantial evidence for putting the organs together might be reinforced. Probably what we managed to learn about the seed, or the male organs, would fully confirm Florin's Cycad idea; but it is at least conceivable that they might prove utterly different and force us to look at *Palaeocycas* in an entirely new light. Even if it were spoilt as a fossil Cycad, it would become a still stranger and more interesting plant.

CYCADOSPADIX AND DIOONITOCARPIDIUM

I next take *Cycadospadix* which for a century has figured in botanical textbooks as one of the best-established representatives of the fossil Cycads. The classic specimens are a dozen isolated fossils scattered in marine Liassic rocks. No doubt they had floated far out to sea and with such fossils association tells you very little. It really looks exactly like a *Cycas* megasporophyll and everyone accepted it as that, though no seed is known attached. I for one would never have doubted it but for one accident. When collecting in the Greenland Rhaetic, I found fossils looking like *Cycadospadix* and which I naturally determined as a species of *Cycadospadix*; a new one as it happened. Then in the course of ordinary routine, I examined the cuticle of my *Cycadospadix* and I was surprised to find that it had all the characters of the Bennettitales and was sharply different from that of any true Cycad. In fact, I convinced myself that my fossils were not seed-bearing megasporophylls at all, but sterile scale leaves; very probably belonging to the flower of a certain one of the associated Bennettitalean leaves.

The original specimens of *Cycadospadix* seem never to have been examined very closely and we certainly know nothing of their fine structure. The nearest thing to a full reinvestigation I know is a pencil note by my own teacher, A. C. Seward, to the effect that the original figures were rather restored and that the specimens did not show clear seed stalks in the way the figures suggested. I hope someone examines *Cycadospadix* critically; I would not be surprised if it proved to be exactly what it has always been supposed to be, but then it might be a sterile scale leaf like my Greenland fossil. *Cycadospadix* certainly does not come into my category of Cycad-like organs supported by a second line of evidence; it is not even as firmly in the category of organs which are clearly Cycad-like just on their own merits as I once thought.

It is only right to mention that Florin, while accepting my fossil as a Bennettitalean scale leaf, decided that it had nothing to do with the other species of *Cycadospadix* and gave it a new generic name. He may be right, but no one can be sure without looking again at the original specimens. The position of another famous fossil Cycad, *Dioonitocarpidium*, is better, but as it seems to me not very secure. *Dioonitocarpidium* has a few rare species from the Keupcr of central and eastern Europe (Lilienstern 1928; Kräusel 1949, 1953). It is primarily the name of a seed-bearing megasporophyll, but a certain leaf has been attributed to it; thus like *Palaeocycas* it has two organs. Also like *Palaeocycas*, it is the subject of a spirited restoration, the stem and megasporophyll being built on to the stem of *Dioon*, the Recent Cycad genus from which it takes its name.

The evidence is, however, much less massive. The leaf is attributed to the megasporophyll on the evidence of association which is said to be impressive, but this time it is not yet supported by anatomical agreement. Then in *Palaeocycas* there was the slightly disconcerting fact that the seeds were missing; here there is the disconcerting fact that, though they are present, they are not quite right or so I feel. The sterile end of the megasporophyll fits very well into the general picture of a *Cycas* or *Dioon* megasporophyll, but the more important fertile end does not fit in well. The bodies at the base are compared with *Cycas* or *Dioon* seeds, but such seeds ought to project and instead they are sunken. In some of the figures the sunken bodies do indeed look like seeds but in others they look more complicated, as though they were sacs enclosing small seeds. These doubts are tiresome for *Dioonitocarpidium* may be just what it is supposed to be and a few solid facts might dispel them all, but without solid facts the doubts remain and it is a duty to retain them.

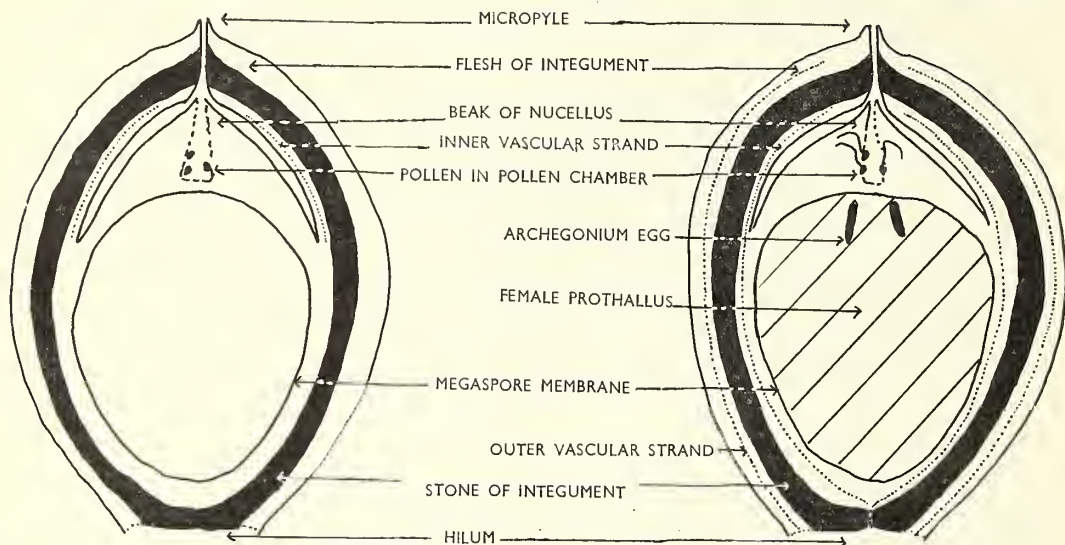
Here solid facts means in the first place microscopic details and we have none at all, and I do not know whether the material is preserved in a way which provides any. When we have such facts, we should be able to relate the leaf and megasporophyll in much the same way as Florin did for *Palaeocycas*. We should also be able to learn about the basal bodies of the megasporophyll; are they in truth simple seeds as supposed or something quite different? If they are quite different, *Dioonitocarpidium* might well disappear from the Cycad alliance.

BEANIA

The next Cycad I take is again synthetic and this time having four important organs—the leaf, the female cone, the seed, and the male cone—it is the most complete. The great gap is the stem (see Harris 1941, Thomas and Harris 1960). The leaf is called *Nilssonia*, a large genus with species occurring in most floras from the Rhaetic to the Middle Cretaceous, sometimes in great abundance. It is again a fairly large leaf of basically pinnate construction as in the Recent Cycads, but it looks rather unlike any Recent Cycad and it was formerly not thought to be specially close to them. For one thing, the lamina is attached to the very top of the midrib instead of being towards the sides, and for another the lamina is rather differently segmented and often divided so irregularly as to look pathological. Recent Cycad leaves delight formal gardeners by their regularity. Then the cuticle, though of Cycad type, is thinner than usual.

Beania, the female cone, was described from excellent specimens a century ago; in fact the first figure dates from 1835 and Carruthers's account that gave the name in 1869 was sensible and compared it properly with a Cycad cone, but after that progress

was arrested and only very gradually did different people contribute crumbs of information from much less good specimens, mostly isolated seeds of half a dozen species. The final synthesis for which I was responsible in 1941 was thus largely a compilation. The reason why Carruthers's account was not fully accepted was in the first place the cone, although fundamentally like certain Cycad cones, does not look like one, being far less compact, and secondly that he did not give any considerable supporting details. It was just one of many hopeful comparisons and the fact that it happened to be supportable failed to convince until that evidence appeared. I give a restoration of the type species



TEXT-FIG. 1. Left, diagram of seed of *Beania gracilis* showing parts so far demonstrated by maceration. Right, generalized diagram of a Recent Cycad seed.

of *Beania* which differs only slightly from the best specimens, so excellent are they. Several Cycad genera have cones like this except that they are compact; in fact, the *Beania* fruit is only technically a cone, it is more like a loose bunch of dates on their stalk.

It is surprising how much structure a compressed seed will reveal when subjected to the ordinary method of destructive maceration; that is to say, slow and uneven destruction which can be stopped when you will. The *Beania* seed (text-fig. 1) shows four distinct cuticles and, with ordinary care, these can be seen in their relative positions. Underneath the outermost cuticle there is a partly disorganized tissue in which scattered fibres occur; and this clearly corresponds to the more or less edible flesh of a Cycad seed, and inside that is a compact woody layer, corresponding to the hard stone. All these layers can be matched fully in Recent Cycad seeds (text-fig. 1).

This is all routine study and ordinary comparison, but I must make a confession. When you have found out all you can hope to see and have interpreted all visible things in a satisfactory way, however sensible it may be to stop, you make a great mistake if you do so. Several times I have gone on blindly, just macerating further seeds without any plan and presently new information appears, perhaps in the twentieth seed, or as with some *Caytonia* seeds after a few hundreds. For some reason occasional specimens

are rather differently preserved and show a feature clearly that is usually so obscure as to be missed. With the *Beania* seed some of this information could have been hoped for, but as it happens is seldom available. For instance, in a cavity at the top of one of the inner cuticles called the nucellus, I was able to find pollen grains. They are just where they would be expected in a Cycad seed some time after pollination and they have burst widely, again as expected, so that although the rather fantastic method of pollen development of a Cycad has not been fully observed in *Beania*, the limited facts are fully consistent with it.

The other observation is of an unpredictable sort. In a few macerated seeds, tiny woody strands are seen sticking to the inner cuticle of the integument (that is inside the stone of the seed). Such strands occur in exactly this position in Recent Cycads but it is not to be expected that they would be seen in *Beania* because they ordinarily decay readily and, even if they do not, maceration destroys them. Here maceration reveals them. It seems that they are casts of tracheids, some sort of resinous matter has impregnated the tracheid walls and showed up their characteristic cast. Need I say the supply of *Beania* seeds gave out before I learnt any more?

I was lucky to have a series of *Beania* cones of various sizes, some of my collecting but most collected by Dr. Hamshaw Thomas nearly fifty years ago. It seems that the *Beania* plant like many plants today shed a lot of its fruits at early stages. When this happens, it is convenient for the fossil botanist because the abortive specimens provide him with a series of young stages reflecting the normal course of development more or less perfectly. The fact these young cones are loose shows that the *Beania* cone is loose all its life, and not like the cones of some plants which are at first compact but later on become loose through the elongation of the cone axis; this elongation making it easier for the seeds to be shed. In the female cones of Recent Cycads, the cone is compact almost all its life. It elongates a little just at pollination time when the scales draw apart leaving small gaps which admit pollen to the seeds, but then it becomes hard and compact again and it remains compact until it is ripe when the cone again elongates a little, making it easier for the animals that eat and distribute the seeds to tear it open. The difference is only one of proportions but it is considerable. Anyone familiar with fir cones would call the female cone of the Recent Cycad, *Encephalartos*, for example, a 'cone', but he would hardly call the *Beania* cone a 'cone' at all. He might rather compare it with a number of dates or currants on their stalk, and I suggest that it has a flexible stalk and hung from a tree branch instead of being borne stiffly erect on a stalk which raises it above the crown of leaves.

The male cones of this plant which are certain species of the old composite genus *Androstrobus* were only recognized recently. This is not so much because it is rare as because it makes an untidy fossil. Anyone who has collected plants where they are abundant as in a coal-measure tip will have been forced to select the best. You reject duplicates and you reject the innumerable black bits that mean nothing and you go on rejecting them until one forces itself on your attention as a definite thing. These particular male cones reveal a good deal of structure and show half a dozen features characteristic of Cycad male cones. They differ in two. They have no stalks, but the Recent cones are always borne on stout erect stalks which raise them clear of the leaf crown. They seem to have been less substantial than the Recent cones, and indeed flimsy. I suggest they hung as catkins from tree branches just like the female cones.

The seed of *Beania* is known attached to its cone, but the other organs are all found separately and they have been assembled in the usual way, on the evidence of association and on the evidence of agreement in structure. The first suggestion came from Nathorst early this century who noticed the association of certain seeds with *Nilssonia* leaves and then several others noticed similar association for various different species. It was Hamshaw Thomas who first pointed out that there was some structural resemblance between *Beania* and *Nilssonia*; and since then both association and agreement in structure have been noted repeatedly for several species in rocks of different stages of the Rhaetic and Jurassic. The structural agreement is most impressive for two Yorkshire species where each has its own specific characters running like a label through the suite of organs. There are a few bits of clinching evidence which are pleasing, though not important; for instance, the same kind of pollen occurs in the male cone as in the seed though that in the seed has germinated.

Proposed reconstruction. I have been slightly unsympathetic about the imaginary stems given by others to their restored Cycads, so it is only decent that I should offer one for their criticism (text-fig. 2). We can be sure the stem was fairly thick, I mean at least 2 cm., because the leaf base is broad; it was also bare and not covered with the bases of dead leaves like most of the Cycads. This again we know because the leaf base was cut off cleanly like the leaves of ordinary dicotyledon trees. In fact, the modern Cycad is unlikely to offer a good model. Instead I take a Dicotyledon tree with thick stems and large lanceolate leaves; the African Shea Butter tree *Butyrrospermum* would do, and there are many others. The leaves are borne on the young apical parts of the stems and behind them are the hanging fruits; we will not follow our model farther since they are botanically unrelated. I believe it differs in another respect; the Shea butter grows in dry country but I think *Nilssonia* must, from its local abundance, have been a dominant tree of the Deltaic swamps or else of the river banks. So far as I know, modern Cycads never dominate such places.

OTHER CASES AND SUMMARY

The final fossil Cycad, which qualifies for inclusion here, is one just described by Thomas and myself. This is the assembly of a leaf and a male cone, and each organ shows Cycad characters. The leaf is *Pseudoctenis lanei* and the male cone *Androstrobus prisma* and as usual they are put together on the evidence of association, in three Yorkshire localities, and on agreement in cuticle structure. In one respect it proves a little disappointing: it shows nothing at all new. The leaf looks exactly like the leaf of several Recent Cycads and agrees very well too in cuticle; and the rather massive male cone could be matched by a bit of the male cone of almost any Cycad. In the absence of any further information, it would be ridiculous to assert that the whole plant agreed with these living Cycads, but it could well be that it does.

There are indeed a great many leaves and some other fossils which have been classified as Cycads in the strict sense and on grounds which I would regard as reasonable. Some look very like the Recent plants, others are rather obviously different and the evidence that they are Cycadean is usually a Cycad-like stoma. Fossil leaves must be described even though nothing more is known about the plant, and they need classification if only for convenience, whether they are known merely from the coarsest facts of gross form,

or with fine microscopic details. It does not matter much if the classification is right, so long as it is reasonably stable and widely accepted. Indeed the improved classification, which results from microscopic study, is chiefly improved in being more nearly botanically correct; to those who will not bother to use a microscope it must be a perfect nuisance.



TEXT-FIG. 2. Restoration of plant bearing *Nilssonia tenuinervis* and *Androstrobus wonnacotti* (left) and young and old cones of *Beania mamayi* (right). The stem is imaginary.

A good many genera of leaves seemed so convincingly like living Cycads when first described that they were named after them, but curiously enough most of these have proved to belong to the Bennettitales. The genera about which we now feel more confident (I think of those mentioned here and also such leaves as *Ctenis*) are not specially similar in gross form, though they agree well in fine structure. But such confidence about an isolated leaf merely means that the limited evidence we have points in a certain way and, even though many agree about it, the position remains the same. Are such leaves as *Ctenis* truly Cycadean?, this means are their undiscovered reproductive

organs and stem sufficiently Cycadean to be fitted into the general Cycad mould? I expect some will, but I sincerely hope they will not all, or else we should have reached the stage in Mesozoic Palaeobotany when no surprises remain.

I will now summarize. The fossil Cycads consist of a good many genera of isolated organs classified on more or less good evidence as Cycadales, a very few genera with two known organs and one genus with more than two organs. If we are right in our synthesis of these plants with two or more organs, and also right in our present classification of, say, half of the isolated organs (and I think it unreasonable to hope for more), then we can say that by Jurassic times the family had probably completed its evolution. It looks as though what happened since was the progressive extinction of important genera and with extinction the impoverishment of the whole family. The nine genera living today are usually placed in two subfamilies, one with *Cycas*, the other with the remaining eight. Both subfamilies were then differentiated, but there was also *Nilssonia* which is worthy of a subfamily of its own; there is nothing to suggest whether there are or are not other subfamilies. The known Jurassic genera are no more primitive than the living ones and they do not help at all in linking the Cycadales with any other family, and for this link one looks first at the Pteridosperms. If we are to find progressive evolution it must be before the Jurassic.

GENERAL CONCLUSIONS

Then I have some general points. I chose the Cycads to illustrate the aims of fossil botany today, but other families would have served instead.

The first point is that in fossil botany we have very broken knowledge. We have separate bits of knowledge about a very large number of separate bits of plants. These separate bits are the ones to which the fossil botanist gives names. Until recently the great majority were the names of leaf species, but now there is an uncontrolled flood of pollen-grain species. I have described quite a number of these one-organ species myself and they are useful and necessary, but their use is almost entirely for the geologist, chiefly as potential zone fossils. Botanically, they are not much good at all. To be sure they are classified, say as Cycads, and when classified are used as evidence that the Cycad family was represented at that time. Then their classification being accepted, morphologists consider them and use them as stages of evolution; but is the classification right? I am now sure that something like nine-tenths of the genera made by the older authors, who gave names implying Cycad affinity, are either mistakenly applied or very doubtful. Why should the ones that I put out hopefully and with an equal feeling of confidence prove right?

My second general point is that the great botanical need is to put together plants out of these organ species. Even a plant with only two known organs is of immensely greater value than the organs taken separately, and after this every item of additional information enhances the value of the whole. In the end, as we approach the whole plant, we get a thing which we can discuss in just the same way as the morphologist discusses his plants: he may consider single organs but he has the whole plant firmly in the background. To be sure there is a drawback; the synthesized fossil plant is the product of an argument based on circumstantial evidence and there is a risk of error. But as fossil botanists know, they have the risk of error always with them.

My third point is that such work as a rule needs special material as well as special laboratory procedure. A preliminary collection *may* give you just what you want; but more likely it just offers a suggestion. It is the same with a collection made by someone else, perhaps years ago. It seldom happens that an early collector knew what specimen I should want to answer my problem today. All too often the missing key specimen is a small and unattractive fossil organ. Then if you want to use the evidence of association, you must go into the field and look and not rely on an uninformed collector. In fact, you must collect, work in the laboratory, and then go back into the field and collect selectively. There was still the tradition a few years ago that the fossil botanist should find his material in a Museum where it had been contributed by a professional collector, and I remember twenty years ago being advised by an old man that to try to collect for myself was a great mistake. Then, of course, the fossil botanist must be willing to do a good deal of hard work in the laboratory and to study the specimens minutely. Some may find this a drawback, but I have always found it the most interesting and rewarding part of my job.

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ALGAL GROWTHS IN THE RHAETIC COTHAM MARBLE OF SOUTHERN ENGLAND

by D. HAMILTON

ABSTRACT. The Cotham Marble horizon in the Upper Rhaetic of southern England includes the two well-known rocks, Landscape Marble and Crazy Cotham Marble. Previous hypotheses concerning the origin of Landscape Marble are listed and the widely quoted gas-bubble explanation is discussed critically. An algal origin is proposed for the Landscape Marble, and the Crazy Cotham Marble is shown to be a current-concentrated breccia.

COTHAM Marble occurs in the Upper Rhaetic Cotham Beds in many localities in South Wales, the Bristol district of southern England and southwards through the Taunton area to Charton and Pinhay Bays on the south coast. It occurs at one horizon only. Two distinct types of Cotham Marble may be present, namely Landscape Marble and Crazy Cotham Marble. Landscape Marble (Pl. 39, fig. 1), known as a geological curiosity for over two centuries, is characterized in vertical section by tree-like structures giving the impression of a wooded landscape. Crazy Cotham Marble is made up of an apparently jumbled mass of slabs and flakes of muddy limestone set in a matrix of similar lithology. Although the two types of limestone usually occur separately, it is not unusual to find them intimately associated.

TERMINOLOGY

Landscape Marble was originally known as Cotham Stone, the name used by Owen (1754, p. 164) in the description of the limestone from Cotham, Bristol, where it is associated with Crazy Cotham Marble. Subsequently the alternative names Landscape or Cotham Marble and Crazy or False Cotham Marble have gained acceptance. Short (1903, pp. 138–9) distinguished seven varieties of Cotham Marble. He proposed that the term Cotham Marble should include all these varieties, reserving Landscape Marble for the variety with aborescent structures and Crazy Cotham Marble for the flaky aggregates. This usage is adopted in the following discussion together with his use of the descriptive terms ‘hedge’, ‘trees’, ‘canopy’, and ‘atmosphere’ for the component parts of the landscape. From the present reinterpretation it will be seen that the additional types distinguished by Short are natural variations of either Landscape or Crazy Cotham Marble.

LANDSCAPE MARBLE

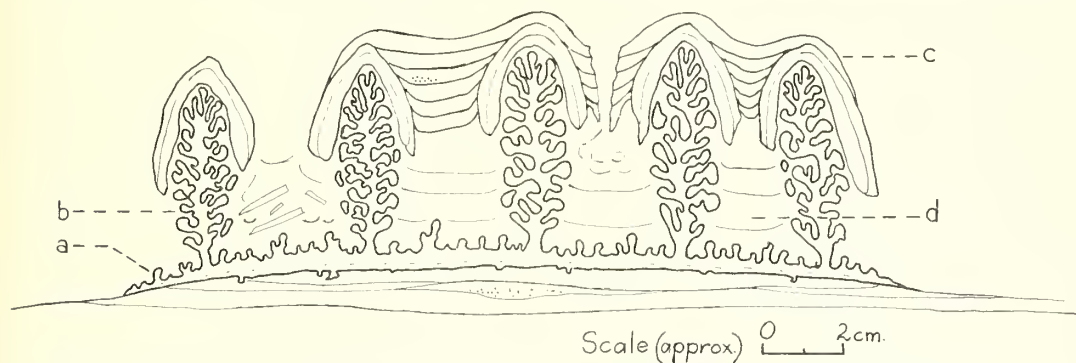
General description. The first description (a very complete one) was given by Owen (1754, pp. 163–78) and Landscape Marble has been discussed subsequently by several writers. Typically it occurs as well-defined lenses or mounds (Pl. 39, fig. 1). The upper surface is irregularly ridged or hummocky (Pl. 39, fig. 2) and is composed of finely laminated material which drapes down the sides of the lens, clearly separating the lens from the enclosing muddy sediments. The size of the lenses varies from about 0.3 to 3.0 metres across and 3 cm. to more than 20 cm. in depth. The landscape rests on

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laminated muddy limestone which often shows small scale sedimentary structures such as scour and fill, sand pockets, and penecontemporaneous deformation structures. The landscape itself is composed of (text-fig. 1):

- (a) The 'hedge'—a basal dark horizon with many small rising projections.
- (b) The 'trees'—arborescent structures rising from the hedge.
- (c) The 'canopy'—finely laminated material bending over the top of the trees and forming the ridged top of the lens.
- (d) The 'atmosphere'—material overlying the hedge, between the trees and below the canopy.

The dark basal horizon is normally continuous and convex upward, being strongly convex towards the margins. The convex surface on which it rests cuts across the laminae



TEXT-FIG. 1. Components of Landscape Marble (Diagrammatic). a, 'Hedge'. b, 'Tree'. c, 'Canopy'. d, 'Atmosphere'.

of the underlying limestone so the whole landscape rises from a low mound of sediments. Typically the height of the hedge averages about 5 mm. and many small projections rise from the upper surface into the atmosphere. The trees rise from the hedge and the branches are lobes or pillars that may be directed upwards, laterally or downwards. The tops of the trees become more foliate or bushy. The height of fully developed trees is surprisingly constant, about 4 to 5 cm. but this often decreases towards the margins of the lens.

The upper surface of the lens has branching ridges and where the sides of the ridges are steep the canopy is often broken between them (Pl. 39, fig. 1). The ridges occur over the arborescent structures so that the latter are not isolated structures but linear, and form a reticulate pattern in plan (Short 1903, p. 137). The crowns of some of the trees have an arrow-head of laminated material draped over them (Pl. 40). The lower edges of the arrow-head fall below the general level of the canopy. There is often an 'unconformity' between the laminae of the arrow-head and the adjacent laminae of the canopy (text-fig. 1). The canopy is normally present immediately over fully developed trees, but where the trees are low a canopy may lie on sediments some distance above the trees (Pl. 39, fig. 1). Usually, however, the canopy closely overlies the trees.

Between the trees there is a light blue-grey indistinctly bedded, muddy limestone descriptively termed the atmosphere. In this the bedding is often bent upwards adjacent

to the trees, sometimes it is horizontal, and Short (1903, p. 137) reports that in some specimens it slopes down a little. Where the canopy is continuous, successive bedding planes can be traced laterally between several trees. Where the canopy is discontinuous this cannot be done. In some cases only the upper beds of the atmosphere are disturbed, but in others the whole atmosphere may show contorted and inclined bedding (text-fig. 1, Pl. 40). Such atmospheres may contain shell fragments, usually concave upwards, and small or even large flakes, similar to those forming Crazy Cotham Marble, which have sunk into the atmosphere (Pl. 40). Some of these flakes bear a hedge.

Landscape Marble occurs most commonly as a single landscape, i.e. with a hedge, trees, atmosphere, and a canopy. In the Bristol area especially it is not uncommon to find two or even three landscapes, one on top of the other. Such rocks are called Double Landscape Marble (Pl. 39, fig. 1) and Triple Landscape Marble respectively. In both Double and Triple Landscape Marble the successive landscapes have a lateral extent almost corresponding to that of the basal landscape, and they often become increasingly convex upwards.

Previous explanations of the origin. These (reviewed by Short 1903, pp. 139–42 and Shrock 1948, pp. 277–9) suggest that the arborescent structures originate from the dark basal horizon and invoke either chemical or mechanical processes.

Short (1903, pp. 142–8) thought the process was chemical accretion, whilst Woodward (1887, pp. 243–4) and Wells and Kirkaldy (1951, p. 203) suggest mineral infiltration. The following mechanical processes have been suggested: rising gas bubbles (Owen 1754 and Thompson 1894), squeezing up along lines of breakage (Fisher, *see* Thompson 1894, p. 410), differential subsidence (Woodward 1901, p. xci), shrinkage of the canopy (North 1930, p. 174), changes in hydrostatic head (Rettegen 1935, p. 288), and density differences (Nettleton 1936, pp. 92–97).

Most of these explanations invoke rather special conditions to account for the well-defined lenses of Landscape Marble. If Landscape Marble is really confined to one stratigraphical horizon these conditions must have been more or less synchronous over an extensive area of southern England. Further, in many places as at Cotham, such conditions must have recurred at precisely the same spot to form the double and triple landscapes.

Of the above processes the only serious contender, and still the most widely quoted, is the gas-bubble hypothesis. In his original description of Landscape Marble Owen (1754, pp. 174–8) suggested that the formation of the rock was due to the rise of gas bubbles trapped in the basal, possibly carbonaceous layer forming the hedge. The rising bubbles carried up organic material to produce the arborescent structures and deform the canopy. Thompson (1894, pp. 401–10) elaborated this idea, suggesting that the gas was formed by decomposition of organic matter in the hedge, and that the canopy was

EXPLANATION OF PLATE 39

Fig. 1. Vertical section through a lens of Double Landscape Marble, showing two landscapes. Locality, Cotham, Bristol. Cb 3850, Bristol Museum Coll.

Fig. 2. Exterior of a lens of Landscape Marble showing branching ridges on the upper surface and the canopy draping down the margin of the lens. Locality, Cotham, Bristol. 14238, Geology Department, Reading University.

Fig. 1

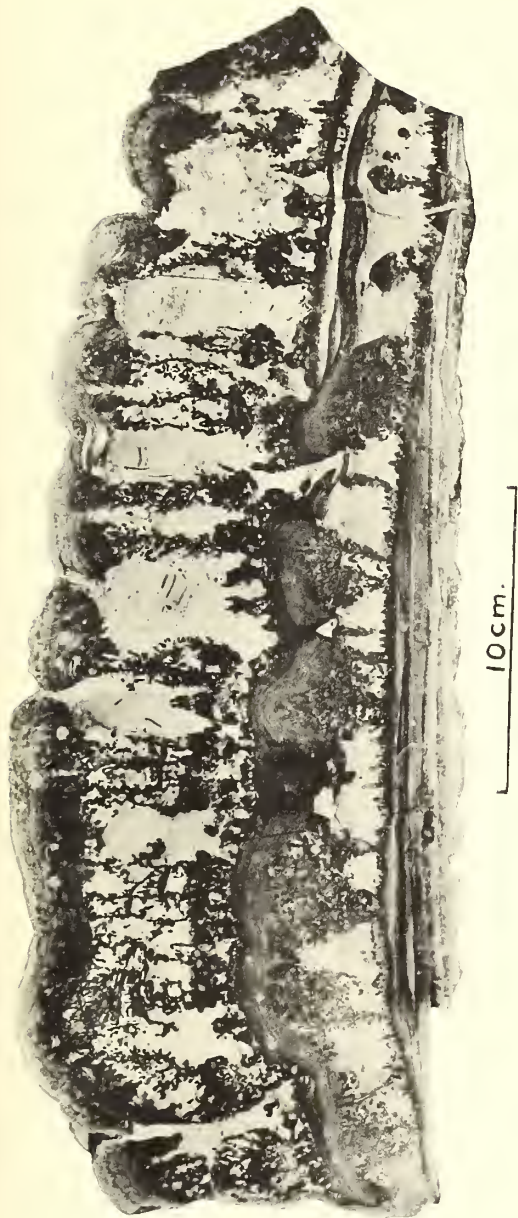


Fig. 2



formed by the outflow and spreading of the decomposed material to completely roof in the arborescent structures.

This mechanism raises many difficulties. Pit and mound or gas-pit structures are not uncommon in sedimentary rocks from which gas has escaped. Despite Twenhofel's statement (1932, p. 682) that pit and mound phenomena could give rise to features similar to those displayed in Landscape Marble, no examples of comparable structures known to have such an origin have been found in the literature. Gases would carry material upwards only on release from moderate pressure. Such a pressure is unlikely to have been attained by burial to a depth of only about 6 cm., the combined height of the trees and the canopy. This depth of burial is certain, for the sediments overlying the lenses do not show deformation sympathetic with the ridges of the canopy. Thus the ridges must have been formed prior to the deposition of the sediments immediately overlying the canopy.

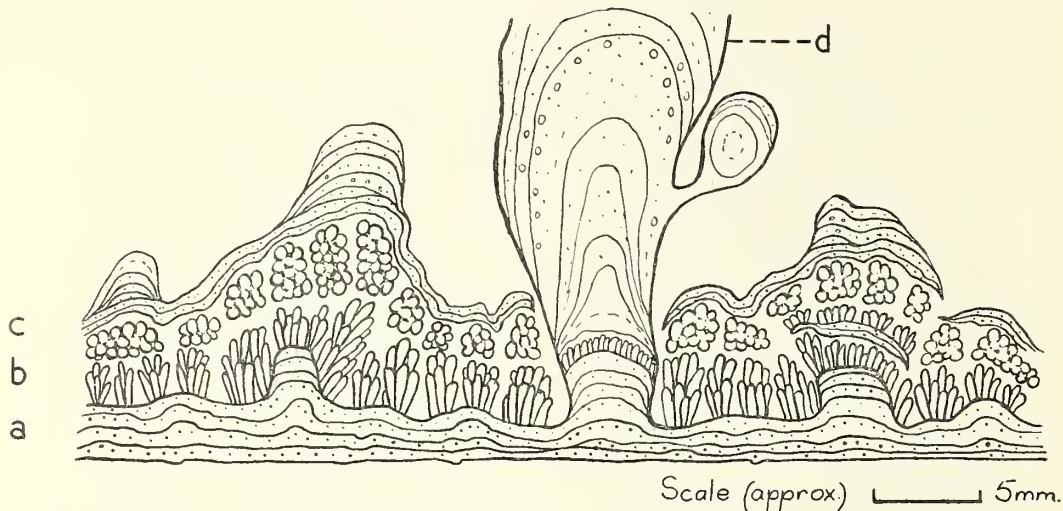
Further, bubbles would tend to rise from random points, whereas the trees have a linear arrangement in plan. Woodward (1892, pp. 110–14), whilst then considering the bubble mechanism possible, sought to explain the linear arrangement of the trees by the rise of organic material along cracks caused by the partial drying of the lower layers. The intimate penetration of even the lower layers of the atmosphere by the arborescent structures (Pl. 41) hardly seems compatible with partial drying out of the sediments. Further, the pattern of the ridges is not typical of desiccation cracks.

Owen also attributed the arching of the canopy to the rise of gas bubbles. This presupposed that the lower layers (the atmosphere) were sufficiently fluid to allow the passage of a bubble whereas the upper layers (the canopy) were relatively coherent and easily deformed. However, in no specimen examined is there any trace at the top of the trees of either the escape of a bubble through the canopy or of a cavity that would indicate the position of the trapped bubble. The canopy forms bifurcating ridges and not domes as would be expected from the rise of gas bubbles. Furthermore, the supposedly deformed canopy is not a normal sedimentary bed for it drapes down the margins of the lens (Pl. 41, fig. 2) and does not extend beyond it.

The source of the gas is attributed to decomposing organic matter in the hedge. To deform the canopy the generation of gas must either have been delayed until the atmosphere and the canopy were laid down, or have continued during the deposition of this material. In the latter case deposition and deformation would have occurred almost simultaneously.

Organic origin. Curiously, no reference has been found directly suggesting an organic origin for Landscape Marble. The lensoid masses with clearly defined margins, in which the marble occurs, strongly suggest organic growth. Further, the forms of the hedge, trees and canopy are not very different from those normally attributed to algal growth. However, Mr. N. E. Butcher, Geology Department, Reading University, has brought to the author's notice, 'Faunal and Lithological Sequence in the Carboniferous Limestone Series (Avonian) of Burrington Combe (Somerset)', in which S. H. Reynolds and A. Vaughan (1911) point out the close similarity of the 'concretionary beds' of S_2 and Landscape Marble. Dr. F. A. Bather and Dr. G. J. Hinde, who examined the S_2 specimens, both suggested that the 'concretionary beds' may be due to calcareous algae. The implication of these interpretations has apparently been overlooked in discussions of the origin of Landscape Marble subsequent to 1911.

Microscopic examination of section shows that the hedge is usually tripartite (text-fig. 2). It consists of: (1) A basal finely laminated horizon, about 1 mm. thick and domed on the upper surface (cf. Anderson 1950, fig. 1B). These undulose laminae are superficially similar to *Malacostroma undulosum* Gürich (1906, pl. xix, figs. 2 and 3). (2) Cylindrical filaments now filled with clear calcite. These rise vertically from the horizontal parts of the basal horizon and radially from the domes. These filaments are overlain by more bulbous ones. (3) Finely laminated encrusting layers, crowning some of these filamentous structures and forming the projections of the hedge. This encrusting



TEXT-FIG. 2. Structure of the 'hedge' (diagrammatic). *a*, Basal laminated horizon. *b*, Zone of cylindrical and bulbous filaments. *c*, Upper laminated layer. *d*, 'Tree'. Drawn from a slide.

layer is apparently similar in structure to the basal horizon (1) and also the canopy over the trees. A comparable relationship of algal structures has been noted in *Stylophycus* by Johnson (1940, pp. 587-9). In this growth-form the digitate pillars are covered with laminae similar to the basal laminae from which the pillars rise.

The trees in Landscape Marble usually rise from the basal laminated horizon of the hedge and pass through the second layer (text-fig. 2). In some cases, however, they develop from the projections of the hedge (Pl. 41). They are thus a complex growth-form of the lower laminated horizons. Convex laminae are present in the lower parts of the trees and may continue into the lobes, cross-sections of which show concentric laminae. Towards the top of the trees there is often a gradual suppression of the laminae as the internal structure becomes patchy or 'flocculent'. These arborescent structures bear some similarity to the branching *Malacostroma plumosa* Gürich (1906, pl. xviii,

EXPLANATION OF PLATE 40

Flakes of Crazy Cotham Marble penetrating Double Landscape Marble. Algal growths encrust some of the flakes and those on the largest flake give rise to arborescent structures. Locality, Cotham, Bristol. Cb 4128, Bristol Museum Coll.



HAMILTON, Cotham Marble

fig. 1), though in Landscape Marble they are more tree-like. They are notably more complex than any of the growth-forms described by Anderson (1950, pp. 5–28).

The canopy is an encrusting algal deposit. It is finely laminated with a flocculent structure between the laminations and appears to be similar to *M. concentricum* Gürich (1906, pl. xix, figs. 2 and 3). The relation of the trees to the canopy is shown in Pl. 41, where laminae of the canopy are seen to be continuous with the structure of a tree. Gürich showed that *M. concentricum* and *M. plumosa* are often associated (1906, pl. xviii, fig. 1, pl. xxii, fig. 2) but he considered these to be two separate forms. The laminae of the canopy in Landscape Marble are most continuous in the upper portions where they can be traced over many ridges to form a sheet blanketing the algal colony. The arrow-heads which penetrate the canopy from below (text-fig. 1, and Pl. 40) suggest that the crowns of the trees were colonized first to form separate canopy ridges. Only subsequently did the canopy spread over the adjacent ridges (text-fig. 1) probably after sedimentation had bridged the gap between the trees. The more even and continuous canopy is therefore a later growth stage than where the ridges are separated by deep depressions.

Where the canopy developed as a continuous sheet it protected the bedded sediments below. In such atmospheres, the up-turned bedding planes adjacent to the trees may be due to the growth of the arborescent structures and/or compaction and lithification. Discontinuities in the canopy may be due either to rupturing of the sheet after its establishment or to incomplete development of the algal sheet between the ridges. The two cases are easily distinguished. Ruptured edges are often irregular and the laminae end abruptly at the break (text-fig. 1). Natural growth edges of the canopy are smooth and the laminae fuse at the margin. Where the canopy ridges remained separate the spaces between the trees were open continuously to sedimentation of clastic and bioclastic material (Pl. 40).

In this figured specimen (Pl. 40) the large flakes penetrate the lower landscape of Double Landscape Marble and are colonized by an algal growth similar to the hedge. Encrusting growths may cover the tops, bottoms, and sides of some flakes. Perhaps algae colonized these flakes prior to their settling into the atmosphere. However, the growth of mature arborescent structures from the large flake shown in this figure suggests the growth of algae *after* the flakes had entered the atmosphere. Often the hedges and trees on flakes encrust the upper ends of the flakes, that is the portion probably standing above sediment level. Development of an arborescent habit is, in all probability, the response to further deposition of sediment. A similar response would account for the development of both the projections on the hedge and the arborescent structures in typical Landscape Marble.

One further feature of the canopy suggests an algal growth-form. Several specimens have been found showing sedimentary material filling small depressions on a former surface of the canopy. The sediment has later been covered by continuous laminae extending into the canopy (text-fig. 1). The light patches (right of centre in the upper canopy of Pl. 39, fig. 1) originated in this way (as also the divided canopy on the lower right of the same specimen).

The convexity of both the hedge and the lens as a whole has been noted above. That of the hedge is determined by the convex sedimentary surface on which it grew. This is probably an eroded surface for it truncates the bedding of the underlying limestone.

Apparently algae colonized such mounds selectively. In many cases the convexity of the lens as a whole is increased towards the margins by the diminution in height of the trees, as in the lower landscape of Pl. 39, fig. 1. Anderson (1950, p. 12) refers to the marked convexity of many algal colonies. He states:

It has been demonstrated that the rate of secretion or precipitation of CaCO_3 by modern algae is dependent on light intensity (Berthold, 1882, p. 419) so that once the convex form is established, the tendency is for the convexity to become more acute, i.e. for the growth to be vertical rather than lateral. This fact that CaCO_3 precipitation usually takes place more rapidly in the vertical axis of the colony provides one criterion by which these organic growths can be distinguished from inorganic structures.

This helps to explain the increasing convexity towards the margins of many lenses of Double and Triple Landscape Marble. Further it has already been noted that the successive landscapes in these forms are similar in size to the basal landscape. The extent of the basal landscape sets a limit to the size of successive landscapes for these are outgrowths of the immediately underlying canopy (Pl. 39, fig. 1). In such cases the later-formed hedge differs from the basal hedge in having no cylindrical or bulbous filaments. The change in habit from canopy to hedge was brought about probably by a change in the rate of sedimentation.

On page 11 of the same article Anderson states:

Regarding the simple growth-forms . . . it is clear that they have very different survival values . . . the following points become evident . . . that the encrusting sheets possess maximum stability but are most vulnerable to burial; that the conical, cylindrical and branching types are most likely the response to a muddy habitat, but are unstable, and therefore probably lived in comparatively quiet waters.

The closely bedded muddy limestone of the Cotham Marble horizon also suggests the general prevalence of quiet water during growth of the algal colonies. Currents, however, did occur, for channels are fairly common in this horizon and Crazy Cotham Marble was obviously formed by current action.

CRAZY COTHAM MARBLE

In spite of the several different explanations advanced to explain the origin of Landscape Marble there has been no such divergence of views concerning the origin of Crazy Cotham. Short (1903, p. 148) interprets the flakes as chemically formed layers later broken by disturbed water conditions.

The flakes are blue-grey muddy limestone weathering like Landscape Marble to a buff colour, and set in a matrix of muddy to sandy limestone. Sometimes the flakes found in a specimen have their long axes aligned, in subparallel fashion, in the major bedding plane. In these specimens the size of the flakes is often fairly uniform. The flakes frequently stand edgewise, displaying a fan-shaped arrangement in vertical sections normal to their long axes. Examination of such sections reveals the typical features

EXPLANATION OF PLATE 41

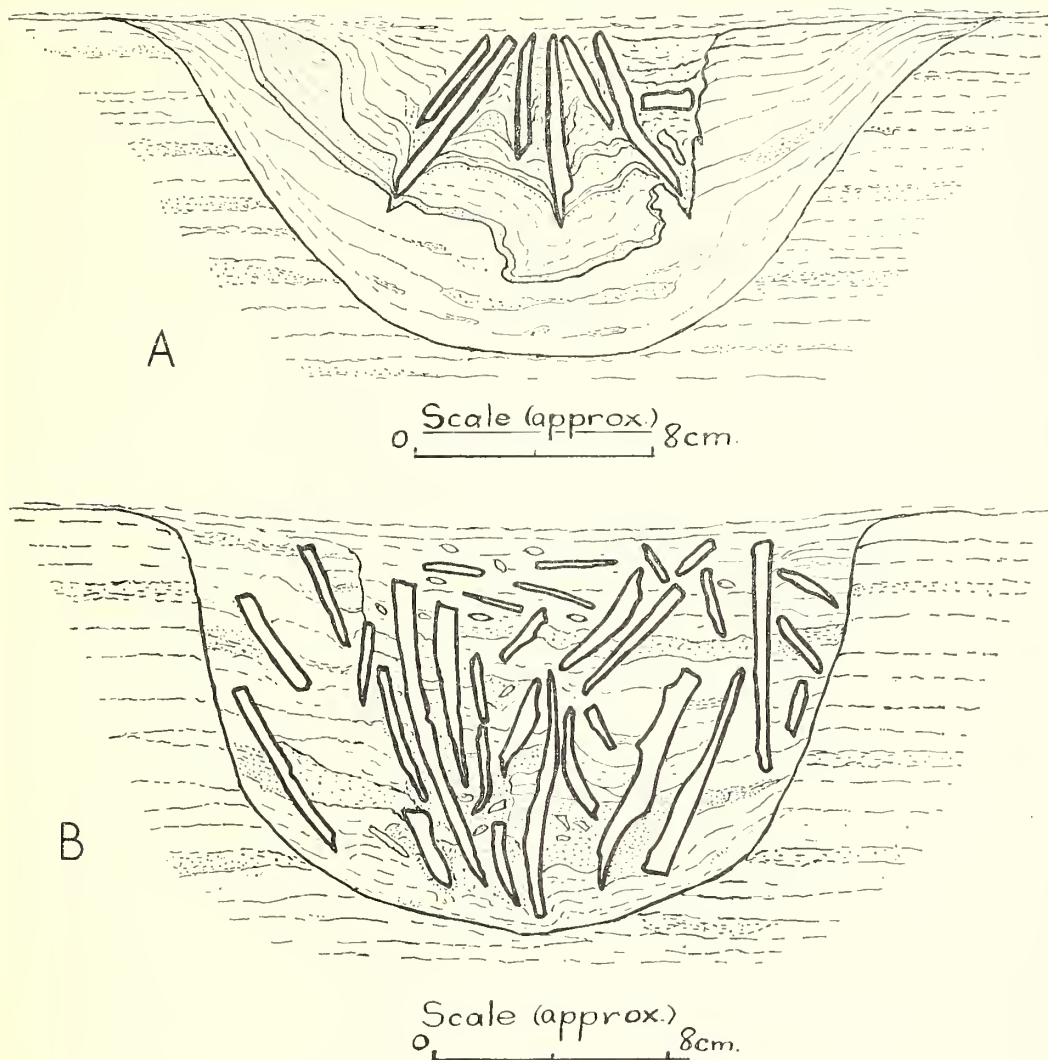
Structure of the algal growths in Landscape Marble. Laminae of the canopy rise from the right-hand margin of the arborescent structure. Growth has been arrested at this stage by the influx of clastic sediment (top) which has buried the algae. The hedge is atypical for there are few basal laminae and few bulbous structures overlying the lower cylindrical filaments. The landscape encrusts a flake. Locality, Lady Hill Road Cutting, Newport, Mon. 14277, Geology Department, Reading University.



○ ————— 5 m m.

HAMILTON, Cotham marble

of eroded channels filled with channel-deposits. The flakes are aligned lengthwise along the channels and penetrate the formerly soft sediment of the channel bottom. The fan-shaped arrangement may be inverted or upright. The inverted arrangement (i.e. con-



TEXT-FIG. 3. The fan-wise arrangement of flakes of Crazy Cotham Marble in channel fillings. A, Inverted fan-wise arrangement. B, Upright fan-wise arrangement. Diagrammatic reconstructions, A from 14239, Aust Cliff, B from 14240, Long Ashton, Bristol.

vergence towards the top) was produced by splaying outwards of aligned flakes sinking edgewise through the watery sediments in a more or less completely filled channel (text-fig. 3A). The upright fan-wise arrangement (text-fig. 3B) was apparently formed by the accumulation of flakes in more open channels. The channel shape and the current in it controlled the arrangement of the flakes.

In both the above arrangements, the flakes probably fell edgewise from above or over the side into the channel, were held by the soft channel-fill and responded like a wind-vane to the currents. Not all flakes in channels are aligned in this fashion. In some specimens the flakes show varying degrees of imbrication, resulting from the rolling of flakes in the channel. Probably alignment parallel to the current persisted only in weak currents whilst faster currents produced imbricated deposits.

As already noted, Crazy Cotham and Landscape Marble may be associated (Pl. 40) for clastic flakes are often trapped between the ridges and lenses of Landscape Marble. Colonization of the Crazy Cotham Marble flakes by a hedge is common but not universal. Short (1903, p. 139) stated that trees never develop from the hedge on Crazy Cotham Marble. However, specimens collected from Pinhay Bay and the specimen illustrated in Pl. 41, show a well-developed landscape rising from Crazy Cotham Marble.

There can be no doubt that the flakes have a mechanical origin and the similarity of their lithology to the enclosing sediments suggests a penecontemporaneous origin from a nearby source. They must have been partially lithified before transport for they retain sharp edges, often penetrate soft sediments and may damage the algal growths in Landscape Marble. Probably the flakes were formed by the drying out of exposed sediment. This is supported by the following characters of the flakes: they have approximately the same thickness, a smooth upper and an irregular lower surface and some are bent (Short 1903, p. 148). The dried flakes were then concentrated by currents to form mud-flake breccias. Anderson (1950, p. 12) observes that the association of breccias and algal beds is quite common.

CONCLUSIONS

Landscape Marble is evidently a biohermal association of algal growth-forms. The hedge, trees, and canopy all have an algal origin, being the structures formed by sediment-binding algae. Probably the bioherms were restricted to a geographical zone (cf. Black 1933, p. 169, Rezak 1957, pp. 145-6) and the features strongly suggest an intertidal environment. Without further information it is not possible to decide if they were strictly coeval throughout the area of outcrop.

Crazy Cotham Marble has a mechanical origin. As the Rhaetic includes much shallow-water sediment it is probable that exposure and drying out took place at different times and places. Hence the presence of Crazy Cotham Marble in itself cannot be taken as evidence of coeval strata without other supporting evidence. Indeed, comparable structures have been noted in the Westbury Beds at Sedbury Cliff.

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LOWER PALAEOZOIC CORALS FROM NEW SOUTH WALES

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ABSTRACT. A collection of corals from an area of some 30 square miles near Wellington, in central-western New South Wales, is described. These comprise twelve rugose and sixteen tabulate species from stratigraphic horizons, ranging from probable Upper Ordovician to Lower or Middle Devonian. Species of the rugose genera *Phaulactis*, *Entelophyllum*, *Disphyllum*, *Palaeophyllum*, *Tryplasma*, *Nipponophyllum*, and *Coronoruga* gen. nov., and the tabulate genera *Heliolites*, *Propora*, *Favosites*, *Multisolenia*, *Striatopora*, *Acanthohalysites*, *Halysites*, *Schedohalysites*, *Falsicatenipora*, *Quepora*, and *Syringopora* are described, and three new species are erected.

THE corals described in this paper were collected from a number of localities and horizons in the parishes of Mumbil and Narragal, on the Bell River some 8 miles south of Wellington (see locality map, text-fig. 1). The area is on the central-western slopes of New South Wales, about 240 miles by road from Sydney.

Joplin (1952) has summarized previous stratigraphic work on the Molong-Wellington region. From the area dealt with in this paper, Etheridge (1907) recorded *Pseudamplexus princeps* (Eth.) from ' . . . Por. 29, Parish Narragal, Molong District, County Gordon; east side of Por. 5, Parish Mumbil, County Wellington . . . '. This species has been regarded as a Lower and Middle Devonian indicator, but both the above localities are now known to be of Middle Silurian age. However, the reliability of Etheridge's reference is uncertain, as the actual specimens are not listed. Hill (1942) lists *?Aulacophyllum* sp. from Portion 105, Narragal Parish. This also is in Middle Silurian limestone. She also lists three other localities of Silurian age, all to the north of Wellington. This is the only palaeontological work to date.

In 1952 very few Ordovician graptolite localities were known in central-western New South Wales. Since then, however, many have been discovered, often in tuffaceous rocks. Sherrard (1954) contains a complete list as then known, and many more have since been found. It appeared from this that the andesitic tuffs and lavas placed by Joplin (1952) in the Middle Silurian, as the Nanima Formation, were all of Ordovician age. Work by the author during 1958, and by Mr. K. J. Kemezys during 1959, has shown that some of these rocks belong to a separate formation, within which the Siluro-Devonian boundary must lie.

The stratigraphy and structure of the area under consideration are shown in text-fig. 1. The Upper Ordovician-Lower Silurian rocks consist of heavily albitized andesitic and basaltic lavas and pyroclasts, detritus from these, together with some limestone lenses (particularly in the Oakdale anticline). The Ordovician graptolites (locality G, text-fig. 1) found and identified are *Climacograptus scharenbergi* Lapworth, *Orthograptus truncatus* var. *intermedius* Elles and Wood, and *Dicellograptus* sp. cf. *elegans* var. *rigens* Lapworth. These correspond to the zone of *Dicranograptus clingani* in the British succession (Elles and Wood 1913). Two unidentifiable diplograptids were also found near locality 247.

No usable graptolites have been found in association with the limestones in this area. Dr. G. H. Packham (in press) has found a similar sequence of lavas and sediments with

thin limestone bands, some distance to the south, 5 miles north-west of Euchareena (locality 'Molong b' in Sherrard 1954, p. 83). The graptolite fauna here contains *Climacograptus bicornis* (Hall), ?*C. scharenbergi* Lapworth, *Orthograptus* sp. cf. *apiculatus* (Elles & Wood), and ?*Lasiograptus harknessi* (Nicholson). These Sherrard places in the zone of *Climacograptus peltifer*. From this it would seem probable that no deposition occurred in the Lower Silurian, the lowermost formation being wholly Ordovician in age.

The overlying massive and detrital limestone contains, in a rich fauna, *Phaulactis shearsbyi* (Süssmilch) and *Entelophyllum latum* Hill, which elsewhere occur in the Wenlockian and Ludlovian (Hill 1940). Halysitids have been found in the base of the limestone; other accurately dated New South Wales limestones with a halysitid fauna do not extend above the Llandoveryan. The age of the main limestone in the area probably, therefore, extends from the topmost Llandoveryan through most or all of the Wenlockian.

Above the limestone is a succession of shales. Near the base is an horizon of grey chert containing *Monograptus bohemicus* (Barrande); this Lower Ludlovian horizon places the top of the limestone at about the Wenlock-Ludlow boundary, and a limestone lens just above the chert (locality 260) as Ludlovian.

A few corals, and *Atrypa* sp., were found in limestone lenses in the overlying andesitic rocks, but proved to be of no stratigraphic use. Above these rocks is a series of calcarenites and shales. Their stratigraphic position and limited fossil content suggested a Lower Devonian age, but this could not be proved. However, to the west of Wellington, in a belt extending south to Molong, are limestones, calcarenites and shales—the Garra beds (Joplin 1952), which are Lower and Middle Devonian in age. During 1959 the author, working in Curra Creek, 9 miles to the west (text-fig. 1), discovered a succession of andesitic tuffs and detrital rocks (many closely resembling those in the Mumbil area) which passed conformably upwards into the Garra beds. This suggests that the calcarenites in the Mumbil area are equivalent to the Garra beds, while the volcanics straddle in time the Siluro-Devonian boundary.

The described fauna, in ascending stratigraphic horizons, is:

1. Upper Ordovician or Lower Silurian. Rugosa: *Palaeophyllum rugosum*, *Tryplasma lonsdalei*, *T. derrengullenense*?, *Nipponophyllum* sp. aff. *giganteum*. Tabulata: *Heliolites daintreei*, group 4, *Propora conferta*, *Favosites gothlandicus*, *Multisolenia tortuosa*, *Acanthohalysites australis*, *Schedohalysites orthopteroides*, *Halysites lithostrotionoides*, *H. sp.*, *Falsicatenipora chillagoensis*, *Quepora bellensis* sp. nov., *Syringopora* sp.

2. Base of the Middle Silurian Limestone. Rugosa: *Phaulactis shearsbyi*, *Palaeophyllum* sp. nov.? Tabulata: *Heliolites daintreei*, group 4, *Propora conferta*, *Multisolenia tortuosa*, *Acanthohalysites australis*, *Syringopora* sp.

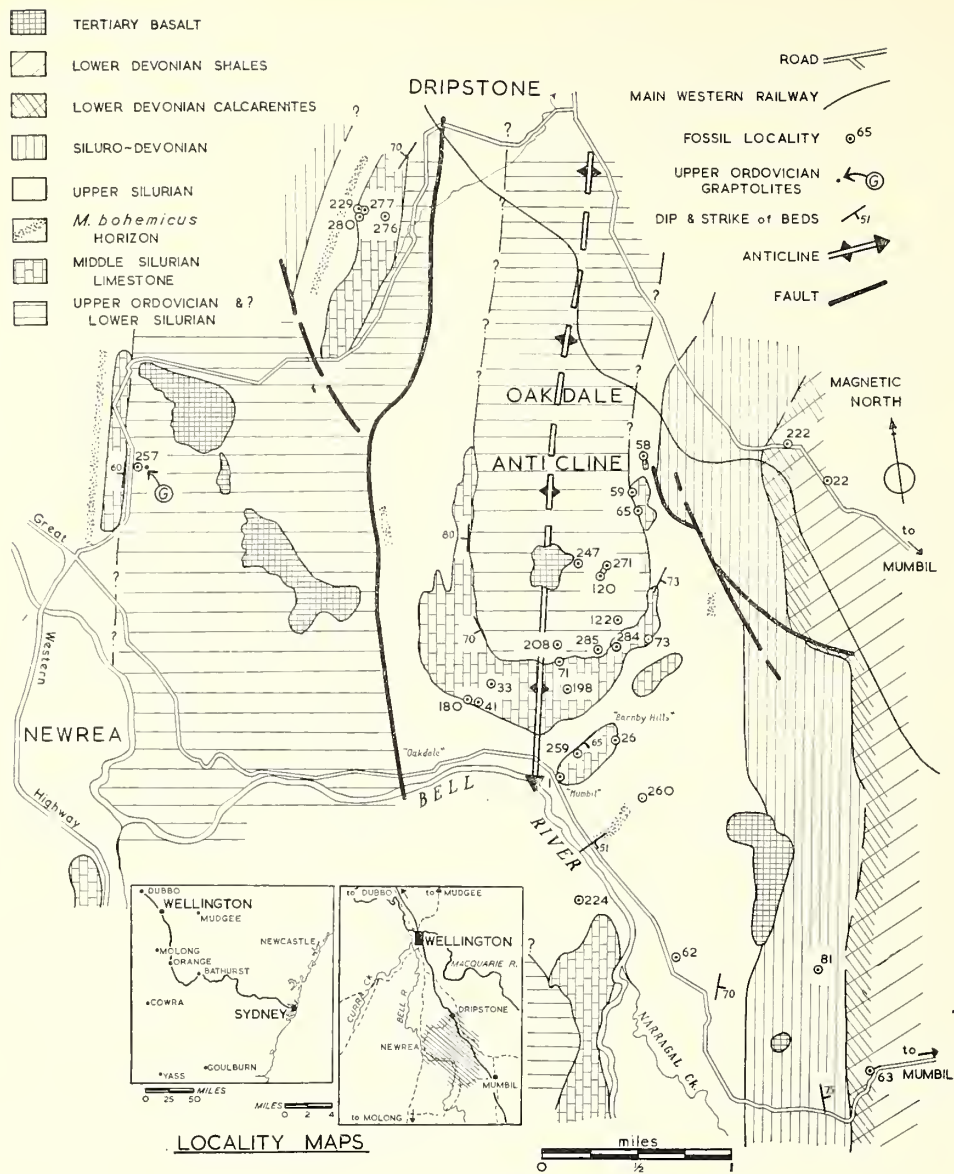
3. Middle Silurian. Rugosa: *Phaulactis shearsbyi*, *Entelophyllum latum*, *Tryplasma lonsdalei*, *T. wellingtonense*, *T. columnare*?, *Nipponophyllum multiseptatum* sp. nov., *Coronoruga dripstonense* gen. et sp. nov. Tabulata: *Heliolites daintreei*, groups 1 and 4, *Propora conferta*, *Favosites allani*, *F. gothlandicus*, *Striatopora* sp., *Syringopora* sp., sp. nov.?

4. Upper Silurian. Rugosa: *Disphyllum* sp. ?aff. *floydense*, *Tryplasma lonsdalei*.

5. Siluro-Devonian (Volcanics). Rugosa: *Tryplasma derrengullenense*?

6. Lower Devonian. Rugosa: *Tryplasma derrengullenense*?. Tabulata: *Heliolites daintreei*, group 3, *Favosites gothlandicus*?, *F. sp.*

In the following pages the term 'variety' is used only when erected previously; its meaning in each case is that of the original author. For simplicity, R. Etheridge, jun., has been referred to as 'Etheridge'.



TEXT-FIG. 1. Geological and locality maps. The inset locality maps show the position relative to Wellington, and in New South Wales. Ruled area on locality map shows the position of the area studied.

'Locality' is abbreviated to 'loc.'; the numbers used are shown in text-fig. 1, and are the specimen numbers used during field work. Specimens with numbers prefixed by 'USGD' are housed in the Department of Geology and Geophysics, University of Sydney. The author would like to thank Professor C. E. Marshall for allowing use of his department's facilities, and Dr. G. H. Packham, Dr. P. J. Coleman, and Mr. F. G. Larminie, all of Sydney University, for much help, advice, and information, and for criticizing this paper. Dr. Dorothy Hill, of the University of Queensland, gave valuable advice regarding *Palaeophyllum* and *Coronoruga*.

SYSTEMATIC PALAEOONTOLOGY

Order RUGOSA

Suborder STREPTELASMATINA Wedekind 1927

Superfamily ZAPHRENTICAE Edwards and Haime 1850

Family HALLIIDAE Chapman 1893

Subfamily LYKOPHYLLINAE Wedekind 1927

Genus PHAULACTIS Ryder 1926

Type species Phaulactis cyathophylloides Ryder 1926.

Phaulactis shearsbyi (Süssmilch) 1914

Plate 42, figs 1, 2

1904 *Cyathophyllum shearsbyi* Etheridge 1904a, footnote, p. 288 (nom. nud.).

1914 *Cyathophyllum shearsbyi* Süssmilch (ex Etheridge MS.), pl. 14B, facing p. 44. Limestone Creek, Bowning district; Upper Silurian (*Barrandella* Shales).

1920 *Cyathophyllum shearsbyi* Süssmilch; Chapman, p. 183, pl. 18, fig. 7; pl. 19, fig. 9.

1935 *Phaulactis shearsbyi* (Süssmilch); Hill, p. 507, fig. 18d.

1936 *Hercophyllum shearsbyi* (Süssmilch); Jones, p. 54, pl. 5, figs. 1a–g; pl. 6, figs. 1a–g; pl. 7, figs. 1h–i, 2.

1940 *Hercophyllum shearsbyi* (Süssmilch); Hill, p. 403, pl. 12, figs. 8, 9.

1942a *Hercophyllum shearsbyi* (Süssmilch); Hill, p. 7, pl. 2, fig. 4.

Material. USGD 10179 (Pl. 42, fig. 1), locality 59; USGD 10185, loc. 65; USGD 10204 (Pl. 42, fig. 2), 10215, 10220, loc. 73; USGD 10281, loc. 198; USGD 11203,–04, loc. 284, Middle Silurian.

Definition. Septa attenuate in dissepimentarium, but dilated at first in tabularium, dilation decreasing from axis outwards during ontogeny, with one early reversal; major septa reach or almost reach axis, and are gently curved; tabularium wide, with gently domed tabular floors, usually of large tabellae; dissepiments small, regular, frequently geniculate. (After Hill 1940.)

Description. The specimens examined are typical of the species. USGD 10215 was the largest corallite collected, being 30 mm. in diameter. The septa are numerous—e.g. USGD 10179 has ninety-four—and thin, some bearing poorly developed zigzag carinae peripherally (USGD 10204, 10179). The major septa interfinger slightly at the axis, and are a little dilated in the tabularium, this dilation decreasing towards the axis. The minor septa extend to the edge of the tabularium, and are half to two-thirds the radius in length. The tabellae are highly irregular, generally sagging.

Remarks. This species, with *Entelophyllum latum* Hill, has so far proved an excellent indicator of the Wenlockian and Ludlovian. It is distinguished from *E. latum* by the axial interfingering and slight twisting of the septa, and the lack of a series of flatly arched tabellae at the outer margin of the tabularium.

Family ARACHNOPHYLLIDAE Dybowski 1873

Subfamily ARACHNOPHYLLINAE Dybowski 1873

Genus ENTELOPHYLLUM Wedekind 1927

Type species by subsequent designation Lang, Smith, and Thomas 1940: *Madreporites articulatus* Wahlenberg 1821.

Entelophyllum latum Hill 1940

Plate 42, figs. 3-5

1940 *Entelophyllum latum* Hill, p. 413, pl. 13, figs. 8-10. Glenbower, Yass; Silurian (Middle?).1942a *Entelophyllum* sp. Hill, p. 4, pl. 2, figs. 1a, b.*Material.* USGD 10212 (Pl. 42, figs. 3-5), loc. 73. Middle Silurian.*Diagnosis.* *Entelophyllum* with numerous thin septa and with axial structure so wide as almost to fill the tabularium (Hill).*Description.* Solitary, with a diameter of 40 mm. There are 102 long septa, the major septa slightly withdrawn from the axis, and the minor septa about two-thirds as long as the major, extending to the inner edge of the wide dissepimentarium. The septa are thin, with zigzag carinae, and there appears to be a small fossula formed by slight deflection of a few major septa within the tabularium (Pl. 42, fig. 4). Dissepiments small, globose, and extremely numerous. Tabulae irregular, mostly incomplete, sagging axially, surrounded by a zone of arched tabellae. The calice is wide and deep, with very steep sides, and with a low, wide, slightly concave axial boss formed by the tabellae and tabulae.*Remarks.* This specimen differs from the holotype in possessing carinate septa and what appears to be a small fossula. Hill (1942a) has described '*Entelophyllum* sp.' from the Gordon River in Tasmania, which is distinguished from *E. latum* s.s. only in possessing carinate septa as in USGD 10212. Hill (1942a) states that '*E. latum*, . . . is without

EXPLANATION OF PLATE 42

Figs. 1, 2. *Phaulactis shearsbyi* (Süssmilch). 1, Longit. sect. of USGD 10179, showing irregular tabellae and septa. Loc. 59. $\times 1.7$. 2, Transv. sect. of USGD 10204. Note recrystallization. Loc. 73. $\times 1.4$.Figs. 3-5. *Entelophyllum latum* Hill. Transv. and longit. sects of USGD 10212. 3, The septa are slightly withdrawn from the axis, as opposed to *Phaulactis shearsbyi* (fig. 2), where they intertwine. Loc. 73. $\times 0.9$. 4, Detail of fig. 3, showing fossula, as indicated by curving of the septa. $\times 2.8$. 5, Showing calice. $\times 0.9$.Fig. 6. *Disphyllum* sp. aff. *floydense* (Belanski). Transv. sect. of USGD 11186. The blurred features, and possibly the darker patches peripherally, are due to heavy recrystallization. For longitudinal section, see text-fig. 2. Loc. 260. $\times 4.1$.Figs. 7, 8, 15. *Palaeophyllum rugosum* Billings. Longit. and oblique transv. sects. of USGD 10240. 7, Note budding corallite (quadripartite, peripheral), upper right. Upper Ordovician (possibly basal Silurian), loc. 122. $\times 1.2$. 8, Tabulae have down-turned edges, and sag slightly axially. Note rare small tabellae. $\times 3.7$. 15, Note occasional incomplete tabulae. $\times 1.2$.Figs. 9, 17. *Coronoruga driptonense* gen. et sp. nov. 9, Longit. sect. of paratype USGD 11103. The epitheca has been removed but there remains a suggestion of the variation in diameter shown by other sections. $\times 1.2$. 17, USGD 11215, paratype, loc. 229.Figs. 10, 11. ? *Tryplasma columnare* Eth. Longit. and transv. sects. of USGD 11197. 10, Note septal spines on right-hand wall. Middle Silurian limestone, loc. 280. 10, $\times 1.7$; 11, $\times 1.5$.Figs. 12, 13. *T. lonsdalei* Eth. 12, Transv. sect. of USGD 10186. As is common, the septa appear as short lamellae. Loc. 62. $\times 3.6$. 13, Transv. sect. of USGD 10201, showing transected septal spines. Loc. 73. $\times 3.6$.Fig. 14. *T. derrengullenense*? Eth. Weathered specimen from flow breccia in ?Lower Devonian volcanics; USGD 10223, loc. 81. $\times 1.9$.Fig. 16. *T. wellingtonense* Eth. Transv. sect. of USGD 10217, showing wide stereozone, long acanthine septa. Loc. 73. $\times 2.5$.



carinae . . .', but in the original description (1940) remarks that paratypes from near the type locality at Glenbower '. . . show septa thickened and with carinae, . . .' and gives no indication that this is of taxonomic significance. Even from a purely stratigraphic viewpoint, separation into two species would be valueless, and taxonomically this would be quite unjustified. Clearly USGD 10212 and *Entelophyllum* sp., from Tasmania, are both *E. latum*. The species is a Wenlock–Ludlow marker.

Family PHILLIPSASTRAEIDAE Roemer 1883
 Subfamily PHILLIPSASTRAEINAE Roemer 1883
 Genus DISPHYLLUM de Fromental 1861

Type species by subsequent designation Lang and Smith 1934: *Cyathophyllum caespitosum* Goldfuss 1826 pars.

Disphyllum sp. ? aff. *floydense* (Belanski) 1928

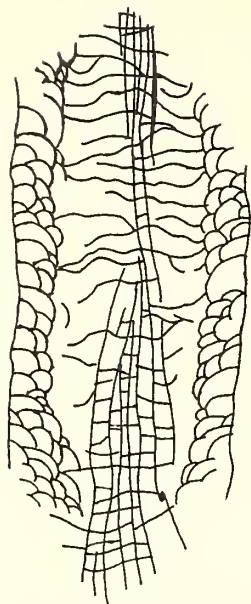
Plate 42, fig. 6; text-fig. 2

Material. USGD 11185, 11186 (Pl. 42, fig. 6; text-fig. 2), loc. 260; probably lower Ludlovian. Associated with *Favosites gothlandicus*.

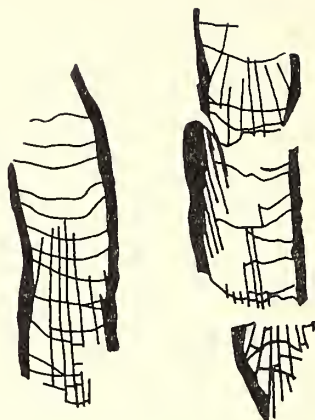
Description. Fasciculate; cylindrical corallites 5 to 8 mm. in adult diameter, the average being 6 mm. The epitheca is marked by fine concentric striae, and by very fine rugae; in many corallites there are constrictions and swellings, the latter sometimes bearing small nodes. The epitheca is quite thin. Septa slightly thickened, the dilation being greatest towards the periphery and sometimes axially also, but it is never marked; unfortunately recrystallization has blurred the septa in places. Where this has not happened, the septa can often be seen to consist of rhabdachanthine trabeculae diverging from a median plane. There are about fifty septa in the adult corallite, the major septa very slightly withdrawn from the axis, and the minor septa one-third to two-thirds as long as the major; the septa may be straight, slightly curved, or somewhat irregular. The tabulae are thin, forming low domes, flat or slightly depressed axially, with a peripheral region where they slope down, and then up again slightly to meet the dissepimental wall; spaced about 10 in 5 mm. Dissepiments in two to four series, small, globose, horizontal peripherally but inclined fairly gently downwards at the inner edge of the dissepimentarium.

Remarks. Externally, allowing for the fact that the corallites are not in their growth position, these specimens resemble *D. floydense*, although the nodes are small and not very numerous. However, the American species has fewer septa (30–34 as against 50), and the arrangement of the dissepiments is a little different; also in many parts of the corallites examined the dissepiments are partly or wholly immersed in a rather dark calcite, which may be sclerenchyme forming a discontinuous peripheral stereozone, although it is more probably an effect of recrystallization. Lacking sections of *D. floydense*, an Upper Devonian species, actual affinities are difficult to determine.

Of the Australian species, the only Silurian one, *D. praecox* (Hill 1940), is half as large again, has only one series of dissepiments, and shorter major septa. *D. curtum* (Hill 1954a) has short major septa. *D. speleanum* (Hill 1950) is smaller, with fewer septa, which are dilated, and a distinctive trabecular arrangement; *D. gemmiforme* (Hill 1940)



TEXT-FIG. 2. *Disphyllum* sp. aff. *Floydense* (Belanski). Longit. sect. of USGD 11186, $\times 7.2$. Traced from photograph; recrystallization is too extensive for reproduction. Interpolation has been kept to a minimum in this and other text-figures.



TEXT-FIG. 3. *Palaeophyllum rugosum* Billings. Longit. sect. of USGD 10245, $\times 3.6$, showing tabulae sagging axially, sometimes incomplete. Tracing of a photograph.

and *D. robustum* (Hill 1942b) both have subequal septa. All these, and several others quite unlike USGD 11186, are Devonian forms.

Suborder COLUMNARIINA Rominger 1876
Family STAURIIDAE Edwards and Haime 1850
Genus PALAEOPHYLLUM Billings 1858

Type species Palaeophyllum rugosum Billings 1858.

Diagnosis. Phaceloid corallites with major septa slightly withdrawn from axis, and short minor septa; narrow peripheral stereozone; tabulae usually complete, flat or axially depressed, may have downturned edges. (See also Hill 1959.)

Remarks. The above classification and diagnosis result from a study of Bassler (1950), and original descriptions of species.

Lang, Smith, and Thomas (1940, p. 94) considered the type species to be 'a phaceloid species of the Streptelasmidae'. Hill (*in* Moore 1956) followed this interpretation, giving the diagnosis: 'Like *Streptelasma* but phaceloid.' Bassler (1950), however, working from Billings' and Lambe's descriptions and figures, considered that the genus is more closely allied to *Favistella* Dana, and so placed *Palaeophyllum* in his family Favistellidae, which is synonymous with the family Stauriidae Edwards and Haime.

Streptelasma is defined by Hill (1956) as possessing a loose axial structure, and axial lobes on the septa. However, published figures of *P. rugosum* (Bassler 1950; Hill 1956; 1959) indicate no such structures. No other species since referred to *Palaeophyllum* has an axial complex or axial lobes; all have simple septa slightly withdrawn from the axis.

Hill (1959), after studying the type species and *P. thomi* (Hall), has reached the same conclusion. She comments also (p. 5): 'This brings into prominence again the question of the generic boundaries between *Favistella*, *Palaeophyllum*, and *Streptelasma*.' It could be that *Palaeophyllum* is a subgenus of *Favistella*, differing essentially in having a phaceloid rather than a cerioid growth form.

Bassler (1950) lists several species of *Columnaria* which he considers to be *Palaeophyllum*. Those described by Soshkina (1936; 1937) certainly are *Palaeophyllum*. These are *P. vulgaris* from the Middle Devonian of the North Urals, and also (1937) from the Upper Ludlovian of the West Urals, with *P. quadrisepitata* (from the latter locality). *P. umbellicrescens* Chadwick (in Williams 1919), from the Lower Silurian of Ontario, Canada, though not figured, disagrees with *Palaeophyllum* in possessing an aulos. However, the specimens Chadwick describes as *Cyathophylloides? williamsi* are certainly *Palaeophyllum*.

Radugin (1936) is not available to me: he described *Columnaria halysitoides* and *C. fascicularis* from the Ordovician (fide Bassler) or Lower Silurian of Western Siberia. If his system of naming was logical, the latter species at least could well be *Palaeophyllum*. If his *C. halysitoides* also turns out to be a *Palaeophyllum*, it will become a junior synonym of *P. halysitoides* (Troedsson). Table 1 necessarily omits Radugin's species, and also *P. stokesi* (Edwards and Haime) which is in need of revision.

Palaeophyllum divaricans Nicholson 1875 has been regarded by later authors as a *Streptelasma*. The major septa are twisted where they meet at the axis, apparently uniting to form a loose axial structure. Nicholson thought it closest to *S. corniculum* Hall. This species is therefore also omitted.

Palaeophyllum rugosum Billings 1858

Plate 42, figs. 7, 8, 15; text-fig. 3

1858 *Columnaria erratica* Billings. Fide Bassler 1950, p. 11.

1858 *Palaeophyllum rugosum* Billings; pl. 1, figs. 6a, b. Little Discharge, Lake St. John, Quebec, Canada. Clermont limestone, Blackriveran or lowermost Trentonian.

1901 *Palaeophyllum rugosum* Billings; Lambe, p. 101.

1950 *Palaeophyllum rugosum* Billings; Bassler, pl. 18, figs. 15, 16.

1959 *Palaeophyllum rugosum* Billings; Hill, pl. 1, figs. 6a, b.

Material. USGD 10240 (Pl. 42, figs. 7, 8, 15), 10244, 10245 (text-fig. 4), 10246, 10248–50, loc. 122; also from loc. 285. Topmost Ordovician or basal Silurian.

Diagnosis. *Palaeophyllum* of mean diameter 5 to 6 mm., with forty septa, the major slightly withdrawn from the axis, the minor short; tabulae with down-turned edges, flat or with wide axial depression.

Description. Phaceloid corallites varying in diameter between 4 and 7 mm., the average adult being 5 to 6 mm. across. There is a narrow peripheral stereozone, about $\frac{1}{3}$ mm. wide. The twenty major septa extend almost to the axis, and may interfinger axially in youth. The minor septa are short, extending at most about one-third the way to the

TABLE 1

Species	Corallite diameter (mm.)	Septa			Tabulae		Range		Remarks
		No. in adult	Relative length		Shape	No. in 5 mm.	Geol.	Geog.	
			major	minor					
<i>P. rugosum</i>	4-7 avge. 5-6	40	$\frac{3}{4}$ R-R	c. $\frac{1}{4}$ R	Flat or sagging axially, with downturned edges	4-5	Om _u -Ou or Sl	N. Amer. and E. Aust.	Type species
<i>P. thomi</i>	2-4.5 avge. 3.5-4	40-44	c. $\frac{3}{4}$ R	$\frac{1}{3}$ - $\frac{1}{4}$ R	Highly arched with axial depression; many incomplete	10-15	Ou _u	N. Amer.	One major septum may extend to the axis, there thickening and turning aside. Stereozone $\frac{1}{3}$ mm. wide.
<i>P. williamsi</i>	3-6 avge. 4	40-50	$\frac{2}{3}$ - $\frac{4}{5}$ R	short	As in <i>P. rugosum</i>	2-5	Sl _l	N. Amer.	Corallites 1-2 mm. apart, with rare connecting processes. Lateral increase
<i>P. halysitoides</i>	3-6 avge. 5	c. 40	$\frac{3}{4}$ R-R	very short	Arched, mostly incomplete	10-14	Ou _u	Greenland	Halysitoid corallum
<i>P. vulgaris</i>	4-7 avge. 5	c. 30	c. $\frac{2}{3}$ R	very short	Irregular, flat, or arched	c. 6	Su-Dm	Ural Mts.	Stereozone 1 mm. wide
<i>P. quadriseptata</i>	7-9 avge. 8	c. 36	$\frac{4}{5}$ R-R	$\frac{1}{2}$ R	Irregular, complete and incomplete, highly arched	?	Su _u	Ural Mts.	Four major septa extend into the axial space, but do not meet
<i>P. troedssonii</i>	5-8 avge. 7	c. 48	R	$\frac{1}{2}$ R	As in <i>P. rugosum</i>	10-14	Ou _u -Sm	Greenland	Septa interfinger axially
<i>P. vaurealense</i>	2.5-3	32	R	$\frac{1}{3}$ R	Thin, depressed axially, flat or downturned peripherally	c. 10	Ou _u	N. Amer.	Septa unite at axis
<i>P. pasense</i>	3-4.5	30	R	'mere ridges'	Arched	7-8	Ou	N. Amer.	Halysitoid corallum
<i>P. pasense parvum</i>	1.7-2	20	R	'mere ridges'	Arched	c. 10	Ou	N. Amer.	May be dwarfed <i>P. pasense</i> —found in shaley dolomite of one locality

axis. Both orders are thin and straight. The tabulae are thin, complete, with very rare small tabellae, and are generally flat, often with down-turned edges, but may be broadly and gently domed or sagging; they are evenly spaced, seven to nine in 10 mm. Increase is quadripartite, peripheral, and apparently parricidal, the young corallites being cerioid shortly after formation (and so completely filling the parent calice).

Remarks. The above diagnosis is based on the figures and data published by Billings, Lambe, and Bassler. The description applies to the numerous specimens collected. Compare Hill (1959 and in press).

Palaeophyllum sp.

Material. USGD 10199, loc. 71. Middle Silurian.

Description. Corallites phaceloid, with an average diameter of 10 mm. There are fifty to sixty thin, straight, lamellar septa, the major septa reaching a little over half-way to the axis, while the minor septa are very short, being mere ridges projecting from a 0.5-mm.-wide peripheral stereozone. The tabulae are thin, and from the three transverse sections obtained appear to be complete, rather irregular, and closely spaced.

Remarks. As can be seen from the table of species above, this is larger than the species so far described; it may well be a new species, but the material is far too limited for one to be erected.

Suborder CYSTIPHYLLINA Nicholson 1889

Family TRYPLASMATIDAE Etheridge 1907

Genus TRYPLASMA Lonsdale 1845

Type species *Tryplasma aequabile* Lonsdale 1845.

Tryplasma lonsdalei Etheridge 1890

Plate 42, figs. 12, 13; text-fig. 4

1890 *Tryplasma lonsdalei* Etheridge, p. 15, pl. 1, figs. 1–6. Hatton's Corner, Yass. Silurian.

1907 *Tryplasma lonsdalei*, with vars. *scalariforme* and *minor*. Etheridge, p. 77, and plates (see Hill 1940).

1937 ?*Tryplasma dendroidea* Etheridge; Hill, p. 151.

1940 *Tryplasma lonsdalei* Etheridge; Hill, p. 406, pl. 12, figs. 13, 14.

Material. USGD 10163, loc. 33; USGD 10164, loc. 41; USGD 10186 (Pl. 42, fig. 12), loc. 62; USGD 10201 (Pl. 42, fig. 13), 10210, 10213, loc. 73; USGD 10280, loc. 180; USGD 10298, loc. 224; USGD 11183 (text-fig. 5), loc. 259. Middle Silurian. USGD 11109, 11117, loc. 247; USGD 11207, loc. 285. Topmost Ordovician or Lower Silurian.

Diagnosis. Phaceloid *Tryplasma* with corallites 6 mm. in average diameter, with connecting process. (Hill 1940.)

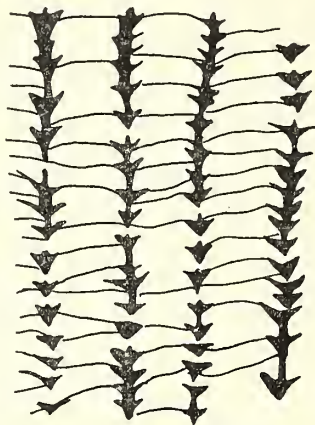
Description. Sub-phaceloid corallites 7 to 10 mm. in diameter. Hill (1940) notes that the average diameter of the corallites in a corallum may be 8 mm., while Etheridge erected his var. *scalariforme* partly on the basis of larger average diameter; unfortunately Hill does not give the limits of variation. There are forty to forty-four acanthine septa, the major extending for one-third to half the radius, while the minor septa are usually quite short, but may be two-thirds the major septa, although always the two orders are

distinct. In transverse section, the spines often do not appear, or are seen only as dots, so that the septa appear short. The spines slant upwards fairly steeply. The peripheral stereozone is quite narrow. The tabulae are flat, complete and regularly spaced some three to four in 5 mm.

Remarks. The size of the corallites, and the regular, distant spacing of the tabulae, agree with Etheridge's 'variety *scalariforme*'; the quadripartite axial increase shown by USGD 11183 (text-fig. 5) supports this. However, Hill (1940) comments that *T. lonsdalei* s.s. can also show quadripartite increase; she also indicates that the size variation could



TEXT-FIG. 4. *Tryplasma lonsdalei* Etheridge. USGD 11183. Drawing, $\times 4$, of budding corallite, showing quadripartite increase. Slightly oblique transverse natural section.



TEXT-FIG. 5. *Favosites allani* Jones. Longit. sect. of USGD 10190, $\times 10.5$. This shows clearly the 'inverted arrowhead' form of the septa. Tracing of photograph.

well destroy the value of the variety. In view of the changes in taxonomic concepts since 1907, and of Hill's comments, it is felt that Etheridge's varieties of *T. lonsdalei* should no longer be used, serving merely to illustrate more completely the range of variation of the species. The species is previously recorded from the Middle and Upper Silurian, and from two localities from the Lower and lower Middle Devonian (Bassler 1950).

Tryplasma wellingtonense Etheridge 1895

Plate 42, fig. 16

1895 *Tryplasma wellingtonense* Etheridge, p. 160; pl. 21, figs. 1-9, pl. 22, figs. 1-5. Wellington Caves. Garra beds; Coblenzian, or ? Couvinian.

1907 *Tryplasma wellingtonense* Etheridge, p. 89, and plates.

1942c *Tryplasma wellingtonense* Etheridge; Hill, p. 187; pl. 5, fig. 10.

1954b *Tryplasma wellingtonense* Etheridge; Hill, p. 112; pl. 8, figs. 16 a, b.

Material. USGD 10217, loc. 73. Middle Silurian.

Definition. Solitary, conical at first, then cylindrical, with repeated rejuvenescence sometimes causing slight change in direction of growth, attaining a diameter of 15 mm. or

more; septal furrows very faint or absent, the epitheca being marked by rejuvenescence or growth rings only. Root-like processes rare. Septa numerous, acanthine, short, set in continuous lamellar sclerenchyme, forming a stereozone 2 mm. wide; tabulae thin, complete or incomplete. (Hill 1954b.)

Description. USGD 10217 is a slightly expanding straight cylindrical corallite reaching 15 mm. diameter with slight rejuvenescence rims. The seventy-two acanthine septa are dilated peripherally to form a stereozone 1 mm. wide, the major septa extending for about half the radius, the inner portions consisting of near-horizontal spines, while the minor septa (likewise spinose) are at least three-quarters the major septa in length. The tabulae are flat, or sometimes irregular, and fairly regularly spaced three to four in 5 mm.

Remarks. This specimen has more septa than the type specimens, approaching *T. derrengullenense* and *T. columnare*. These, however, have short septa and spinose tabulae, and differ somewhat in size. Etheridge's solitary species require extensive revision. The species has previously been recorded from the Coblenzian and Couvinian of two localities only; the known range is thus extended from the Middle Silurian to the lower Middle Devonian.

Tryplasma columnare? Etheridge 1907

Plate 42, figs. 10, 11

1907 *Tryplasma columnaris* Etheridge, p. 85, and plates. Molong district; Garra beds, Lower-Middle Devonian; Quedong, Co. Wellesley; Silurian.

1940 *Tryplasma columnare* Etheridge; Hill and Jones, p. 187; pl. 3, figs. 3, 4.

Material. USGD 11197, loc. 280. Middle Silurian.

Description. Maximum diameter 16 mm. There are fifty-eight septa, equal in length at 1.0 mm., dilated to form a peripheral stereozone 0.5 mm. wide. The tabulae are complete, flat or slightly irregular, or sometimes incomplete. They do not appear to bear trabeculae.

Remarks. Differs from the specimens described by Etheridge in the narrow stereozone and the more regular tabulae lacking trabeculae. However, the corallite is sediment-filled and somewhat recrystallized, and this may have destroyed most of the trabeculae. Differs from *T. derrengullenense* in the short, subequal septa and the more regular shape, without rejuvenescence. Hill and Jones (1940) record a corallite of the same size from limestone near Wellington Caves, of probable Devonian age.

Tryplasma derrengullenense? Etheridge 1907

Plate 42, fig. 14; Plate 43, fig. 12

1907 *Tryplasma derrengullenense* Etheridge, p. 88; pl. 22, figs. 5-8. Limestone Ck., Bowning. Silurian.

1940 *Tryplasma derrengullenense* Etheridge; Hill, p. 407; pl. 12, fig. 16.

Material. ?USGD 10159, loc. 22, Lower Devonian. USGD 10223 (Pl. 42, fig. 14), loc. 81. Topmost Silurian or Lower Devonian. USGD 11173 (Pl. 43, fig. 12), loc. 257. Upper Ordovician or Lower Silurian.

Diagnosis. Solitary, trochoid or ceratoid *Tryplasma*, with irregular rejuvenescence, and a very deep calice. (Hill 1940.)

Description. The specimens are all weathered fragments of corallites, the septal spines being visible only in USGD 11173 (Pl. 43, fig. 12), and so identification has had to be made largely on the basis of size, number of septa, and depth of the grooves left by the weathering of the septa. USGD 10159 has twenty septal grooves in an arc of about 60 deg. and so had some 100 to 120 at a diameter of about 25 mm. The deeper grooves marking the major septa have been taken as indicating *T. derrengullenense*, although the size and number of the septa are greater than described by Etheridge or Hill. Rejuvenescence is not visible, the fragment being very small.

USGD 10223-c has ninety septa, the major apparently longer than the minor, at a diameter of 15 mm., while USGD 10223-b (Pl. 42, fig. 14) shows a marked rejuvenescence rim. USGD 10223-d has an epitheca marked by faint concentric growth circles and septal grooves, but this comparative smoothness could be due to wear before burial. The corallite is 18 mm. in diameter over the rejuvenescence rim, and the major septal spines (seen in an oblique polished surface) are 2 mm. long.

USGD 11173 has twenty-two septa in an arc of about 80 deg., i.e. about 100 at a diameter of some 10 mm. The major septa are thick, rather long spines arising from short septal lamellae, while the minor septal spines are short and blunt, arising directly from the corallite wall. The nature of the septa indicates *T. derrengullenense*, although the diameter is small.

Remarks. USGD 10159 occurs in the shales above the Siluro-Devonian volcanics; stratigraphical relations to the west of Wellington indicate equivalence to the Lower and Middle Devonian Garra beds. USGD 10223 comes from either a flow breccia or an agglomerate in the volcanics. USGD 11173 comes from a marl near the Ordovician graptolite locality, and so is either Upper Ordovician or Lower Silurian in age. The species is recorded only from the Silurian of the Yass-Bowning district.

Family CYSTIPHYLLIDAE Edwards and Haime 1850

Genus NIPPONOPHYLLUM Sugiyama 1940

Type species *Nipponophyllum giganteum* Sugiyama 1940

Nipponophyllum multiseptatum sp. nov.

Plate 44, fig. 12; Plate 45, fig. 9

Material. Holotype USGD 11099, loc. 224; portion 141 (330 yards N. of por. 105, 330 yards W. of Bell R.), parish of Narragal, county Gordon. Paratype USGD 10299. Middle Silurian.

Diagnosis. *Nipponophyllum* with sixty septa, the minor half as long as the major, in corallites 10 to 15 mm. in diameter, with a peripheral stereozone, and a zone of tabellae at the edge of the tabularium.

Description. Fasciculate corallum composed of corallites 10 to 15 mm. in diameter, the average being 12 mm.; corallites contiguous or but slightly separated. Thirty discontinuous septa of each order, the major septa reaching three-quarters of the distance to the axis, while the minor septa are about half as long. The major septa appear to be more continuous than the minor septa, particularly axially, while all the septa are set in

a sclerenchymal peripheral stereozone up to 1 mm. wide, which may extend on to the dissepiments. The dissepimentarium consists of one or two rows of rather large, globose, downward sloping dissepiments separated from the narrow tabularium by a circlet of irregular arched tabellae. The tabulae are usually flat, complete and incomplete, spaced about five in 5 mm. The calice is rather deep, with a flat floor and very steep sides. Increase is by lateral budding.

Remarks. As well as size, the narrow tabularium surrounded by a zone of tabellae distinguishes this species. It is much larger than *N. colligatum* (Hill), and differs from *N. giganteum* Sugiyama in the distinction of major and minor septa. Hill (1954a) has described a coral from the Yarrongobilly Caves which may be conspecific with this. Hill likens the coral to *Nipponophyllum*, but suggests that the appearance of discontinuity in the septa 'may be due to crushing on one side of the fragment'.

Horizon. A small limestone lens in shale, laterally equivalent to the Middle Silurian limestone.

Nipponophyllum sp. aff. *giganteum* Sugiyama 1940

Plate 43, figs. 3, 4; Plate 45, fig. 12

Material. USGD 10289, loc. 208. Topmost Ordovician or Lower Silurian.

Description. Phaceloid corallum of corallites 6 to 12 mm. in diameter, the average being 9 mm. The corallites are touching, or buttressed by irregular connecting processes formed as outgrowths of the dissepimentarium. The thirty to thirty-six equal, discontinuous septa consist of discrete trabeculae arising from the dissepimental surfaces, which may or may not pierce several dissepiments; the septa extend some two-thirds of the distance to the axis. The dissepimentarium consists of two to four rows of unequal, irregular but roughly globose dissepiments, sloping sharply down towards the axis. The tabulae are generally incomplete, sagging deeply, and irregularly spaced, about five or six in 5 mm.

Remarks. The specimen is very similar to *N. giganteum*, differing in the smaller number of septa—although this is very variable—and the slightly smaller average diameter.

Genus *CORONORUGA* gen. nov.

Type species *Coronoruga dripstonense* sp. nov.

Diagnosis. Large solitary corallites with a wide dissepimentarium separated from a rather narrow tabularium by an aulos in which are embedded short, discrete trabeculae.

Remarks. This genus shares its characteristic of discrete trabeculae only with *Hedströmyllum* Wedekind 1927, *Holmophyllum* Wedekind 1927 (considered by some to be the same genus; see Hill 1940, p. 397), and *Mazaphyllum* Crook 1955. Of these, the first two are simple, and the last thamnasteroid, and in all three the trabeculae occur in the dissepimentarium, piercing several dissepiments. All lack an aulos, and both of Wedekind's genera have a small tabularium unlike that of *Coronoruga*. That of *Mazaphyllum* is very similar, although smaller, and this, plus the geographical relationship, suggests that *Mazaphyllum* is the closest to *Coronoruga*.

Coronoruga dripstonense sp. nov.

Plate 42, figs. 9, 17

Material. Holotype USGD 11104, loc. 229. Boundary of portions 194 and 116, 500 yards west of Neurea-Dripstone road, Parish of Mumbil, County Gordon, Wellington. Paratypes: USGD 11103 (Pl. 42, fig. 9), 11212, 11213, 11214, 11215 (Pl. 42, fig. 17), 11216, loc. 229. USGD 11195, 11198, loc. 280. Middle Silurian.

Diagnosis. *Coronoruga* of diameter 20 to 25 mm., the aulos generally being 1 to 2 mm. thick and about 10 mm. in diameter, with numerous small dissepiments and many axial and peripheral domed tabellae.

Description. Most of the corallites collected have had their epitheca worn off, but those retaining it show that it is thin, with a large number of longitudinal striae (septal grooves?) about 1 mm. apart. The maximum diameter measured is 25 mm. (USGD 11212), but it appears from a longitudinal section of USGD 11216 that the diameter is rather variable, although the diameter of the aulos remains constant. In this section the dissepimentarium varies in width from 5 to 8 mm. This kind of variation is seen in the holotype, although the epitheca is missing.

The aulos varies in thickness between 0.5 and 2.5 mm., but is usually about 1 mm. thick. It is made up of lamellar sclerenchyme, and the trabeculae pierce this, causing the lamellae to curve in towards the axis. The trabeculae arise a little in from the outer edge of the aulos, and may protrude into the tabularium for $\frac{1}{4}$ mm., although usually less; they apparently are arranged in a large number of vertical rows, in which their vertical spacing varies from $\frac{1}{4}$ to 1 mm. None of the sections is good enough (due to recrystallization) to allow counting of the septa.

The tabulae are irregular, arched or sagging, with many large, globose tabellae both axially and peripherally, always highly domed. They are thin, but most are coated with a layer of sclerenchyme up to $\frac{1}{2}$ mm. thick. The dissepiments also bear this coating of sclerenchyme, and are globose, usually small, but sometimes large and elongate; they slope down towards the axis, the inclination increasing towards the aulos, where they are often vertical and somewhat compressed. There are no trabeculae in the dissepimentarium.

EXPLANATION OF PLATE 43

Figs. 1, 2, 5, 6. *Heliolites daintreei* Nicholson and Etheridge. 1, 2, Group 1 of Jones and Hill 1940. Transv. and longit. sects. of USGD 10165. Loc. 58. $\times 3.6$. 5, 6, Group 4, USGD 10211, loc. 73. $\times 10.2$.

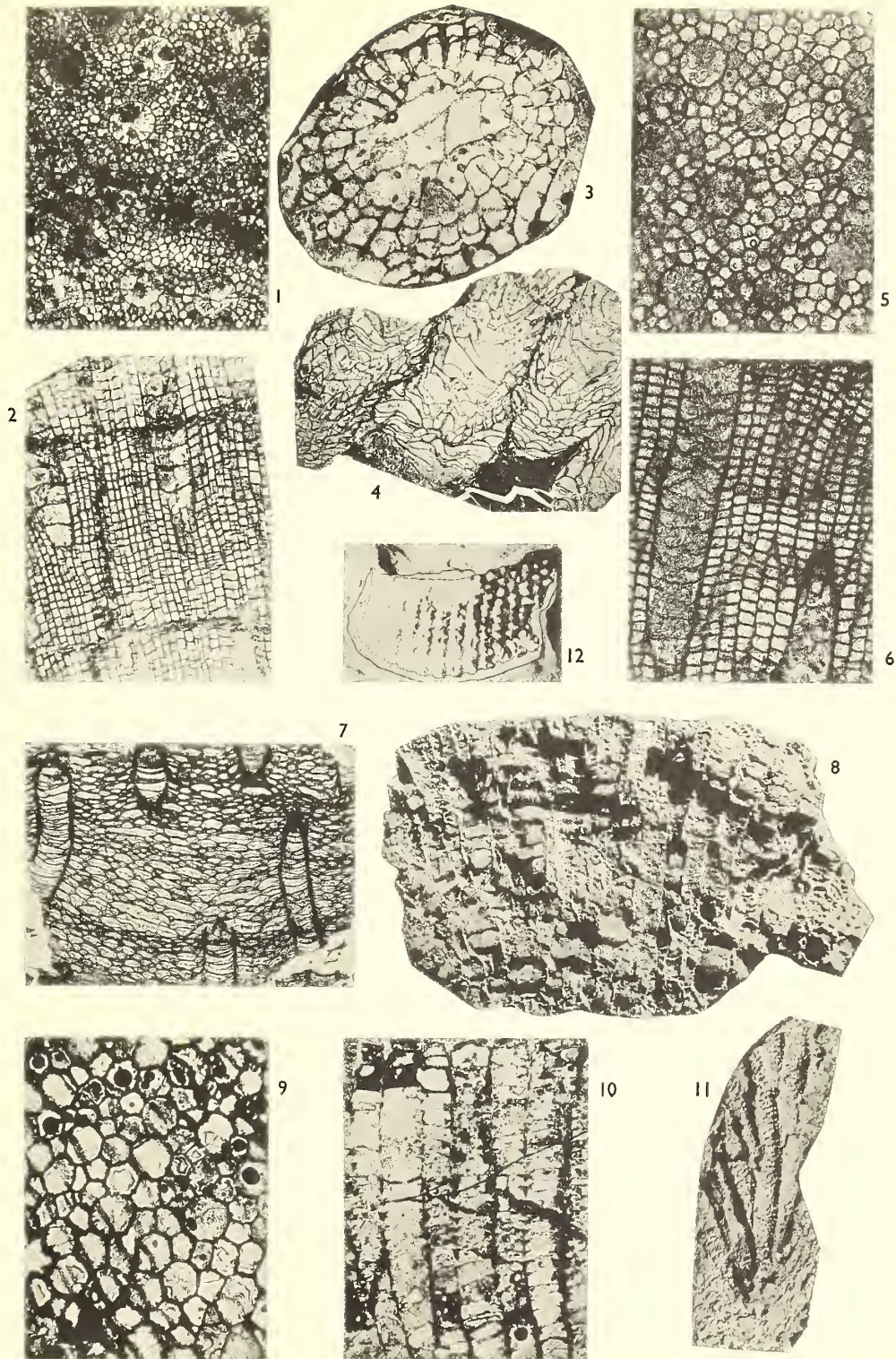
Figs. 3, 4. *Nipponophyllum* sp. aff. *giganteum* Sugiyama. 3, One corallite enlarged to show form of septa. $\times 3.4$. 4, Longit. sect. of USGD 10289. $\times 1.8$.

Fig. 7. *Propora conferta* Edwards and Haime. Longit. and oblique sections of USGD 11174. Note discontinuities in the wall of the lowest tabularium, characteristic of the species. Loc. 257. $\times 3.6$.

Figs. 8–10. *Favosites allani* Jones. 8, Natural longit. sect. of silicified corallum, USGD 10209, showing numerous septal spines and regular tabulae. Loc. 73. $\times 3.5$. 9, 10, Transv. and longit. sects. of USGD 10190. The corallum is heavily silicified. Note mural pores, lower middle of fig. 10. $\times 3.5$.

Fig. 11. *Favosites* sp. Natural longit. sect. of USGD 10294, showing numerous small, blunt septal spines. Loc. 222. $\times 3.3$.

Fig. 12. *Tryplasma derrengullenense*? Eth. Low oblique view of USGD 11173, showing short septal spines, the major proceeding from short lamellae, the minor directly from the wall of the corallum. The exposed portion of the corallum has been outlined with ink. Loc. 257. $\times 3.7$.



Order TABULATA

Family HELIOLITIDAE Lindström 1876

Subfamily HELIOLITINAE Lindström 1876

Genus HELIOLITES Dana 1846

Type species Astraea porosa Goldfuss 1826.*Heliolites daintreei* Nicholson and Etheridge 1879

Plate 43, figs. 1, 2, 5, 6

1940 *Heliolites daintreei* Nicholson and Etheridge; Hill and Jones, p. 201; pl. 8, fig. 5.1943 *Heliolites daintreei* Nicholson and Etheridge; Jones, p. 37; pl. 1, figs. 9, 10.1954a *Heliolites daintreei*? Nicholson and Etheridge; Hill, p. 40; pl. 4, fig. 10.1954b *Heliolites daintreei* Nicholson and Etheridge; Hill, p. 115; pl. 9, fig. 30.

Remarks. Jones and Hill (1940) divide the species into four ill-defined groups, of which three are represented in the described faunas.

Group 1. USGD 10165, loc. 58; Pl. 43, figs. 1, 2. Middle Silurian. Tabularia with thin walls round or somewhat crenulate, as thin as tubuli walls; diameter varies between 1.5 and 2.0 mm., the mean of twenty-five being 1.7 mm. Tabularia separated by two to six rows of tubuli, centre-centre distance varying between 2.5 and 4 mm. Tubuli polygonal, may have perforate walls. Septa thin, arising from the crenulations of the tabularial walls, with long spines, slanting steeply upwards, reaching halfway to the axis. Tabulae thin, flat, five to seven in 5 mm. Sola twelve to fifteen in 5 mm., thin, flat or sometimes oblique. Has fewer tabulae than the specimens described by Jones and Hill.

Group 3. USGD 10187, loc. 63; Lower Devonian. Thick-walled tabularia with crenulate walls, with long septal spines arising from the crenulations, and curving sharply upwards to approach the axis. Tabularia vary from 1.0 to 1.2 mm. in diameter, the mean being 1.1 mm.; they are separated by one to five rows of polygonal tubuli with walls thick, but thinner than the tabularial walls; centre-centre distance 1.4 to 2.8 mm. Tabulae thin, flat, eight to seventeen in 5 mm. (observed variation). Sola flat, spaced fourteen to twenty in 5 mm.

Group 4. USGD 10168, loc. 59; USGD 10196, loc. 65; USGD 10203, 10211 (Pl. 43, figs. 5, 6), loc. 73; Middle Silurian. USGD 11124, loc. 247. Upper Ordovician or Lower Silurian. The tabularia have walls a little thicker than the tubuli walls; they are crenulate, with long upcurved spines arising from the crenulations. The tabulae are thin, flat or concave, sometimes incomplete, and may bear spines. The tubuli are irregularly polygonal or rounded, sometimes vermiform. This is a very variable group as can be seen from the metric data:

Specimen	Tabularial diam. (mm.)			Distance (in mm.) between tabularial centres	Tabulae in 5 mm.	Sola in 5 mm.
	min.	max.	average			
USGD 10168	2.8	3.2	3.0	3.0 to 5.0	6-18	15-20
USGD 10196	1.0	1.2	1.1	1.0 to 2.5	5-8	18-20
USGD 10203	1.5	2.0	?	2.5 to 4.5	?	?
USGD 10211	0.5	0.8	0.6	1.0 to 2.0	10-15	c. 20
USGD 11124	1.5	2.0	?	2.0 to 3.5	7-10	15-20

USGD 10196 has slightly broad-based septa, but otherwise agrees with the description of Jones and Hill.

Subfamily PLASMOPORINAE Wentzel 1895
Genus PROPORA Edwards and Haime 1849

Type species *Porites tubulatus* Lonsdale 1839 pars.

Propora conferta Edwards and Haime 1851

Plate 43, fig. 7

1851 *Propora conferta* Edwards and Haime, p. 225. Borkholm, Russia. *Fide* Jones and Hill 1940.

1899 *Plasmopora australis* Etheridge, p. 33; pl. A, fig. 11; pl. B, figs. 5, 6.

1899 *Propora conferta* Edwards and Haime; Lindström, p. 93; pl. 8, figs. 32–39; pl. 9, figs. 1–23, 31, 32, 35. *Fide* Jones and Hill 1940.

1920 *Plasmopora australis* Etheridge; Chapman, p. 185, pl. 28, fig. 28.

1927 *Plasmopora shearsbyi* Dun, p. 262, pl. 21, figs. 5, 6.

1940 *Propora conferta* Edwards and Haime; Jones and Hill, p. 209; pl. 11, figs. 3–5.

Material. USGD 10199, loc. 71; USGD 10215, loc. 73; USGD 11180, loc. 259; Middle Silurian. USGD 10235, loc. 120; USGD 11125, loc. 247; USGD 11174, loc. 257 (Pl. 43, fig. 7); USGD 11189, loc. 271; USGD 11210, loc. 285. Upper Ordovician or Lower Silurian.

Description. Tabularia 1.0 to 1.5 mm. in diameter, separated by 0.5 to 2.5 mm. of coenenchyme. The tabularial walls are thick, often highly crenulate, with short discontinuities; the crenulations may extend into the coenenchyme as ridges for as much as $\frac{1}{2}$ mm., but are usually short, and sometimes non-existent. The tabulae are generally flat and complete, ten to twenty-five in 5 mm., but may sag slightly, and may be incomplete. The sola are globose, small, numerous; occasionally there occur rather elongate, larger sola. Coenenchymal trabeculae could not be found in any of the sections cut.

Remarks. This species is characterized by the frequent occurrence of discontinuities in the tabularial walls.

Family FAVOSITIDAE Dana 1846
Subfamily FAVOSITINAE Dana 1846
Genus FAVOSITES Lamarck 1816

Type species *Favosites gothlandicus* Lamarck 1816.

Favosites allani Jones 1937

Plate 43, figs. 8–10; text-fig. 5

1937 *Favosites allani* Jones, p. 90; pl. 12, figs. 4, 5. Silurian (*Barandella* shale), Yass.

1940 *Favosites allani* Jones; Hill and Jones, p. 189; pl. 5, figs. 1a, b.

Material. USGD 10190 (Pl. 43, figs. 9, 10), ex alluvium, 'Mumbil' homestead; USGD 10209 (Pl. 43, fig. 8), loc. 73. Middle Silurian.

Diagnosis. *Favosites* with small corallites, with numerous septal spines which are short, horizontal, and with a broad base, with small circular mural pores typically in one row, and with thin, horizontal, and usually complete tabulae, twelve to seventeen in 5 mm. (Hill and Jones 1940).

Description. USGD 10209 is a fragment some 3×2 cm., in which the polygonal corallites are 1.0 to 2.0 mm. in diameter, thin-walled, with numerous septal spines about 0.1 to 0.2 mm. long, sometimes in the form of small squamulae. The mural pores are not frequent, but are circular, 0.1 to 0.2 mm. in diameter, sometimes with a squamula immediately above. The tabulae are flat, usually regularly spaced seven in 5 mm., with one or two cycles of septal spines between each pair of tabulae.

USGD 10190 is a portion of a silicified massive corallum 5 cm. across and 3 cm. deep. The corallites vary in diameter from 1.0 to 2.5 mm., the mean of twenty-five being 1.4 mm.; most are 5- or 6-sided, but some have 3, 4, 7, or 8 sides, and may be rather irregular. The walls are 0.05 to 0.15 mm. thick, although recrystallization has often increased this, and obscured the detail. They are pierced by mural pores 0.1 to 0.2 mm. across, arranged in one or two rows (depending mainly on the width of the wall), and spaced vertically 0.4 to 0.6 mm. apart, one cycle between each two tabulae, and often with a septal spine or squamula directly above. Often these will be coincident in two adjacent corallites, forming an inverted arrowhead above the mural pore (text-fig. 5). The septa are numerous, short (up to 0.4 mm. long), and rather thick, with broad bases; they are horizontal, or pointing gently upwards. The tabulae are flat, thin, regularly spaced ten to fifteen in 5 mm.

Remarks. USGD 10190 differs from described specimens in the increased frequency of double-row mural pores. The specimen is from alluvial wash just north-east of the junction between the Mumbil-Neurea road, and portions 3 and 5, Parish of Mumbil, near 'Mumbil' Homestead; it is almost certainly derived from the top of the Middle Silurian limestone, where there are numerous similarly preserved fossils. USGD 10209 comes from near the top of the Middle Silurian limestone. The species is recorded from the Upper Silurian of Yass and the Lower or lower Middle Devonian Garra beds opposite Wellington Caves.

Favosites gothlandicus Lamarck 1816

Plate 44, figs. 1, 2

For early synonymy see Hill and Jones 1940, pp. 191-4.

1954a *Favosites gothlandicus* Lamarck, formae *gothlandicus* and *forbesi*; Hill, p. 42; pl. 4, figs. 13, 14.

Material. ? USGD 10160, loc. 22; Lower Devonian. USGD 10221, loc. 73; USGD 11196 (Pl. 44, figs. 1, 2), loc. 280. Middle Silurian. USGD 10251, loc. 122; Upper Ordovician or Lower Silurian.

Diagnosis. *Favosites* with very large, thin-walled prismatic corallites, few septa, complete rather distant tabulae, and two rows of large, circular mural pores.

Description. USGD 10160 is the impression of a small fragment in mudstone. The polygonal corallites are 1.5 to 2.0 mm. in diameter, with thin walls bearing a few short, thick septal spines, pierced by rare mural pores in one or two rows. The tabulae are spaced seven in 5 mm.

USGD 10221 is portion of a massive corallum in which the thin-walled prismatic corallites vary in diameter between 1.5 and 2.5 mm., the average being about 2 mm. Septal spines are short, and very rare. The mural pores are 0.2 to 0.3 mm. in diameter,

in two rows except on narrow walls, and usually *en echelon*, although sometimes parallel. The tabulae are flat, rarely concave, spaced fairly regularly four or five in 5 mm.

USGD 11196 is also massive. The corallites are 2 to 3 mm. in adult diameter, with frequent new corallites arising at the junctions. The walls are irregular in thickness, varying from 0.02 to 0.2 mm., and are slightly crenulated, the crenulations frequently bearing septal spines. These are numerous, closely spaced vertically, short, with broad bases, and inclined upwards. Mural pores in two rows, *en echelon*. There are somewhat discontinuous zones of wall thickening, often associated with tabular crowding. The tabulae are flat, or with median depressions, occasionally inosculating in the zones of crowding. Spacing varies from seven to fourteen in 5 mm.

USGD 10251 is a roughly hemispherical corallum about 8 cm. across. The corallites have slightly thickened walls, and are 1.0 to 3.0 mm. in diameter, the average being about 2 mm. The mural pores are sparse, usually in two rows, parallel, and rather small. The septal spines are short and thick. Tabulae flat, four to seven in 5 mm.

Remarks. USGD 10221 probably belongs to the forma *gothlandicus*. USGD 11196 differs from the normal in its zones of wall thickening and tabular crowding, the occasionally inosculating tabulae, and the slight wall crenulations. The species has been previously recorded from the Silurian and Lower Devonian.

Favosites sp.

Plate 43, fig. 11

Material. USGD 10294, loc. 222. Lower Devonian, calcarenites above the Siluro-Devonian lavas.

Description. A fragment of a ramose corallum with thick-walled corallites about 1 mm. in diameter. The septal spines are numerous, short, and blunt, and are not regularly arranged. There are no mural pores, and the remains of the tabulae appear to be widely spaced.

Remarks. Of the species tabulated by Hill (1940) the only one of comparable size with septa and widely spaced tabulae is the specimen figured as *F. alpinus* by le Maître.

Genus MULTISOLENIA Fritz 1937

Type species *Multisolenia tortuosa* Fritz 1937.

Multisolenia tortuosa Fritz 1937

Plate 44, fig. 3

1937 *Multisolenia tortuosa* Fritz, p. 231, text-figs. 1-6. Lockport formation, Ontario. Silurian.

1937 *Paleofavosites mirabilis* Tchernychev, pp. 86, 117, pl. 7, figs. 4a-c.

1956 *Multisolenia tortuosa* Fritz; Stearn, pp. 65-66, pl. 5, figs. 1-4.

Material. USGD 10178, loc. 59. Middle Silurian. USGD 10291 (Pl. 44, fig. 3), loc. 208. Upper Ordovician or Lower Silurian.

Diagnosis. *Multisolenia* with corallites 0.25 to 0.6 mm. in diameter, thin walls, and close, thin, slightly convex tabulae.

Description. USGD 10178 is an irregularly stratiform mass, while USGD 10291 is a radiating corallum in the form of a low inverted cone 12 cm. across and 5 cm. deep, the

apex being $\frac{3}{4}$ cm. across. In both the corallites are rounded, with thin walls. Multiplication is as indicated by Stearn (1956), as also are the solenia, which are regularly and closely spaced giving broken surfaces a distinctly beaded appearance. They are 0.25 mm. in diameter and ten in 5 mm. The tabulae are very thin, and are often obscured or destroyed by recrystallization; they are slightly arched, 0.25 to 1.0 mm. apart.

Subfamily PACHYPORINAE Gerth 1921

Genus STRIATOPORA Hall 1851

Type species Striatopora flexuosa Hall 1851.

Striatopora sp. Hill and Jones 1940

Plate 44, figs. 4, 5

1940 *Striatopora* sp. Hill and Jones, p. 200; pl. 8, figs. 3a-c. Crystal Springs, Molong. Garra beds, lower Devonian.

1954a ? *Striatopora* sp. Hill, p. 44; pl. 4, figs. 19a-b. Silurian.

1954b ? *Striatopora* sp. Hill, p. 115; pl. 9, figs. 28a-b. Lower to Middle Devonian.

Material. USGD 10152, loc. 1; USGD 10162 (Pl. 44, figs. 4, 5), loc. 26; USGD 10164, loc. 41; USGD 11190, loc. 276. Middle Silurian.

Description. Ramose coralla 6 to 25 mm. in diameter, the average being 10 to 15 mm. Corallites irregularly polygonal; diameter 0.5 to 1.5 mm. axially, where the walls are thin, pierced by mural pores 0.2 to 0.3 mm. across, apparently arranged in one row. This axial zone, where the corallites are nearly parallel, is one-third to two-thirds the corallum diameter, and towards its edge the corallites start to curve outwards, finally turning abruptly horizontal in a peripheral zone where the walls become dilated, and the tabulae at first become crowded, and are then replaced by a plug of sclerenchyme, sometimes interrupted by a couple of tabulae. The dilated walls are pierced by two rows of mural pores, about $\frac{1}{2}$ mm. apart; the corallites increase in diameter to 2.0 mm. This zone is usually 1 or 2 mm. thick. Axially the tabulae are flat and distant, six to ten in 5 mm. In the zone of crowding they may be four in 1 mm. Septal spines are sparse and short, often obscured by recrystallization.

Family HALYSITIDAE Edwards and Haime 1850

Subfamily HALYSITINAE Edwards and Haime 1850

Genus ACANTHOHALYSITES Hamada 1957

Type species Halysites australis Etheridge 1898.

Diagnosis. Halysitinae with septal spines in macrocorallites, with both mesocorallites and microcorallites, and most palisades with more than one macrocorallite.

Acanthohalysites australis (Etheridge) 1898

Plate 44, figs. 6, 7

1898 *Halysites australis* Etheridge, p. 78; pl. 17, figs. 1-8, Bell R., Wellington. Silurian.

1904 *Halysites australis* Etheridge, p. 29; pl. 6, fig. 4, pl. 7, fig. 6, pl. 9, figs. 1, 2.

1957 *Acanthohalysites australis* (Etheridge); Hamada, p. 404.

Material. USGD 10183 (Pl. 44, figs. 6, 7), loc. 59. Middle Silurian. USGD 11211, loc. 285. Topmost Ordovician or Lower Silurian.

Diagnosis. *Acanthohalysites* with loose, spreading corallum; fenestrules large, variable, with smooth sides; palisades of two to twelve corallites, which are oval, rather small, with twelve long septa and close, complete, irregular tabulae; microcorallites narrow, oblong, with distant tabulae; walls thick.

Description. The fenestrules are irregular in shape, at times labyrinthine. The corallites have thick walls, and are 0.75 to 1.0 mm. long by 0.5 mm. wide; the septal spines reach over half-way to the axis, and are arranged in vertical rows, five on each wall and one at each end of the corallite. The tabulae are flat, fifteen to twenty in 5 mm. The microcorallites are not always present, but where developed are slit-like in transverse section, causing no waisting of the palisades; their tabulae are distant.

Genus HALYSITES Fischer von Waldheim 1813

Type species *Tubipora catenularia* Linnaeus 1767.

Halysites lithostrotonoides Etheridge 1904

Plate 44, figs. 8, 9

1904 *Halysites lithostrotonoides* Etheridge, p. 23; pl. 1, fig. 1, pl. 4, figs. 1, 2, pl. 9, fig. 4. Spring Ck., Molong. Lower Silurian.

1920 *Halysites lithostrotonoides* Etheridge; Chapman, p. 187.

1957 *Halysites lithostrotonoides* Etheridge; Hamada, p. 402.

Material. USGD 10227, loc. 120. Topmost Ordovician or basal Silurian.

Diagnosis. *Halysites* with regular, pavement-like fenestrules, and smooth-walled palisades of one to five oblong corallites, flat-ended, 0.75 to 1.0 mm. long and $\frac{1}{3}$ mm. wide, separated by thin rectangular microcorallites. Tabulae ten in 5 mm., and twenty in 5 mm. in microcorallites.

Description. The corallites are often somewhat larger than in Etheridge's specimens, reaching 1.25 mm. in length, although the average is about 1 mm., but the flat-ended

EXPLANATION OF PLATE 44

Figs. 1, 2. *Favosites gothlandicus* Lamarck. Transv. and longit. sects. of USGD 11196. Loc. 280. $\times 3.5$.

Fig. 3. *Multisolenia tortuosa* Fritz. Transv. sect. of USGD 10291. Upper half of fig. retouched to show meandroid tabularia. Loc. 208. $\times 10.9$.

Figs. 4, 5. *Striatopora* sp. Hill and Jones. Transv. and longit. sects. of USGD 10162. 4, Negative print showing mural pores in peripheral zone. Loc. 26. 4, $\times 2.7$; 5, $\times 1.4$.

Fig. 6. *Acanthohalysites australis* (Eth.). 6, Transv. sect. of USGD 10183. Loc. 59. $\times 1.8$. 7, Enlargement of portion of fig. 6, showing septa. $\times 10.5$.

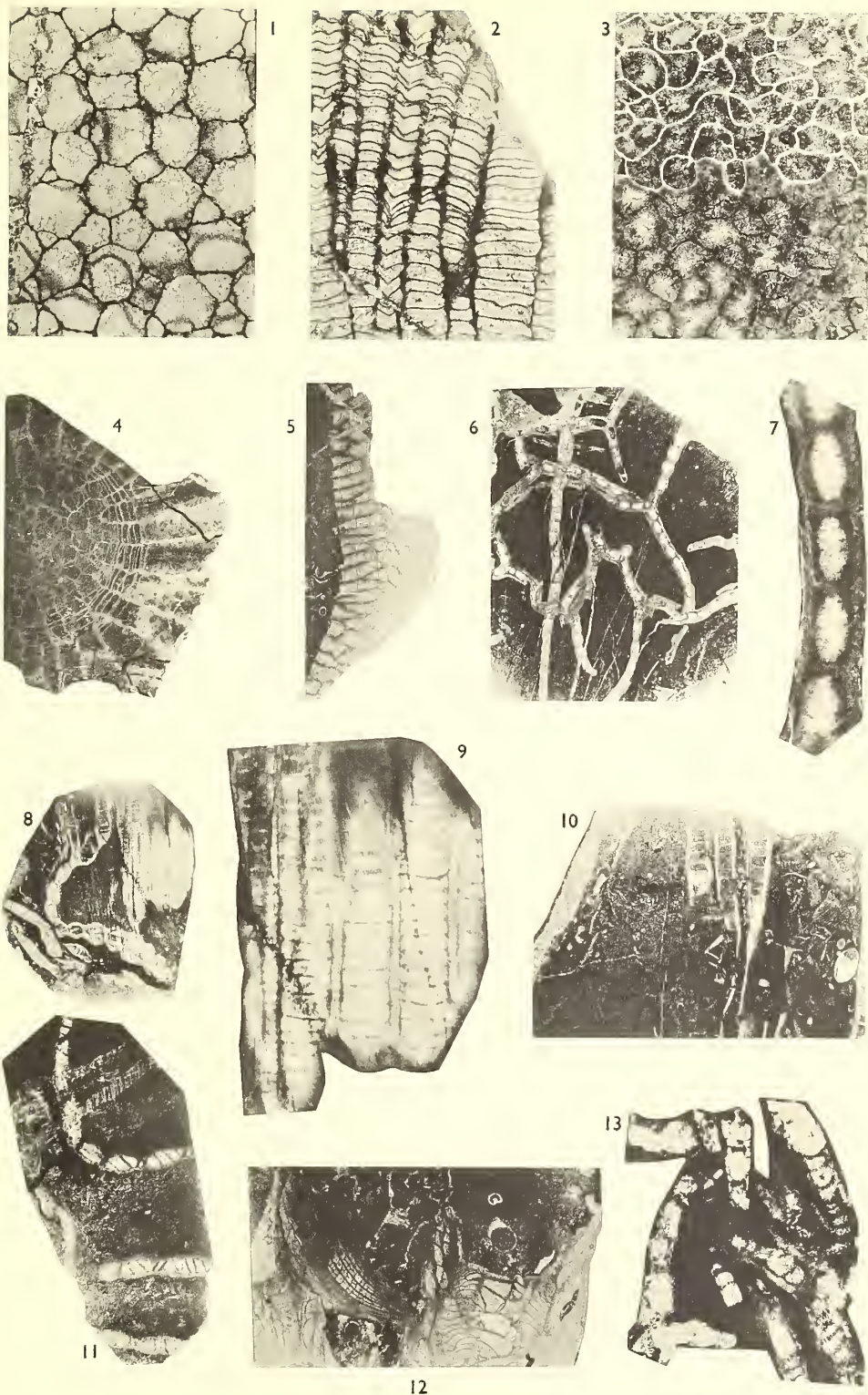
Figs. 8, 9. *Halysites lithostrotonoides* Eth. 8, Longit. and oblique transv. sects. of USGD 10227. Loc. 120. $\times 1.8$. 9, Enlargement of portion of fig. 8, longit. sect. $\times 5.1$.

Fig. 10. *Schedohalysites orthopteroides* (Eth.). Longit. sect. of USGD 11188. Loc. 271. $\times 3.4$.

Fig. 11. *Halysites* sp. Oblique transv. sect. of USGD 11115. Loc. 247. $\times 3.5$.

Fig. 12. *Nipponophyllum multiseptatum* sp. nov. Longit. sect. of holotype, USGD 11099. Note lateral bud, with relatively continuous major septa and discontinuous minor septa. Also shows form of calice. Loc. 224. $\times 1.9$.

Fig. 13. *Falsicatenipora chillagoensis* (Eth.). Transv. and oblique longit. sects. of USGD 6923. Septa can be distinguished in the transv. sects. of corallites, lower left, arranged as in *A. australis* (fig. 7). $\times 6.5$.



oblong shape is distinctive, particularly in hand specimen. There is slight corrugation of the palisades, accentuated in oblique sections. The fairly regular pavement-like fenestrules are also distinctive. The tabulae are regular, slightly concave, fifteen in 5 mm., in the corallites, and flat, twenty to twenty-five in 5 mm., in the microcorallites, which are about $\frac{1}{4}$ mm. long. The corallite walls are slightly thickened.

Halysites sp.

Plate 44, fig. 11

Material. USGD 11115, loc. 247. Topmost Ordovician or Lower Silurian.

Description. A small portion of an irregularly radiating corallum, in which the fenestrules, distally, are polygonal or somewhat irregular. There are two to six corallites to a palisade; they are 1.25 to 1.5 mm. long and 0.75 to 1.0 mm. wide, oval, aseptate, with flat tabulae spaced fifteen in 5 mm. The microcorallites are rectangular, 0.5 mm. wide and about $\frac{1}{4}$ mm. long, causing some waisting of the palisades. The corallite walls are thick.

Remarks. Differs from *A. pycnoblatooides* in absence of septa and somewhat narrower corallites. *H. süssmilchi* has labyrinthine fenestrules and more widely spaced tabulae.

Subfamily SCHEDOHALYSITINAE Hamada 1957

Genus SCHEDOHALYSITES Hamada 1957

Type species *Halysites orthopteroides* Etheridge 1904.

Diagnosis. Halysitidae in which microcorallites and mesocorallites are not present in all parts of the corallum.

Schedohalysites orthopteroides (Etheridge) 1904

Plate 44, fig. 10

1904 *Halysites orthopteroides* Etheridge, p. 25; pl. 3, figs. 1, 2, pl. 7, figs. 4, 5. Wellington district. Silurian.

1920 *Halysites orthopteroides* Etheridge; Chapman, p. 188; pl. 25, figs. 22, 23, pl. 26, fig. 24.

1957 *Schedohalysites orthopteroides* (Etheridge); Hamada, p. 401.

Material. USGD 11188, loc. 271. Topmost Ordovician or Lower Silurian.

Diagnosis. Halysitid with irregular fenestrules, palisades corrugate, of two to nine oval corallites 1–1 $\frac{1}{4}$ mm. by $\frac{3}{4}$ –1 mm.; aseptate, with irregular tabulae ten in 5 mm.; microcorallites mere slits or absent, about twenty tabulae in 5 mm.

Description. Fragments only have been examined. The corallites are 1.0 to 1.5 mm. long and 0.75 to 1.0 mm. wide, oval, with fairly thin walls. There are no septa, and the thin, flat tabulae are spaced twelve to fifteen in 5 mm. The palisades are waisted at the microcorallites.

Genus FALCICATENIPORA Hamada 1958

Type species *Halysites japonicus* Sugiyama 1940.

Diagnosis. Schedohalysitinae with mesocorallites but without microcorallites.

Falsicatenipora chillagoensis (Etheridge) 1904

Plate 44, fig. 13

1904 *Halysites chillagoensis* Etheridge, p. 36; pl. 5, figs. 3, 4, pl. 8, fig. 3, pl. 9, fig. 3. Mungana, Chillagoe, Queensland.

1957 *Catenipora chillagoensis* (Etheridge); Hamada, p. 400.

1958 *Falsicatenipora chillagoensis* (Etheridge); Hamada, p. 98.

Material. USGD 6923, loc. 122. Upper Ordovician or Lower Silurian.

Diagnosis. Fenestrules large, irregular, smooth-sided; corallites long-oval, thick-walled, two to twelve per palisade, with stout septa which recrystallization may obscure. Poorly developed mesocorallites.

Description. Corallum radiating; the fenestrules are quite irregular in shape, with smooth sides. The palisades usually have only three or four corallites, but this may increase as the corallum grows—the only specimen found is a small, incomplete corallum. The corallites are rather small, being 1.0 to 1.5 mm. long and 0.5 to 0.75 mm. wide, the average being on the smaller side. The wall separating them is usually thin, but may be as thick as the palisade walls which are up to 0.25 mm. at corallite centres. Septa may occasionally be seen as irregular protrusions from the walls, but are mostly obscured by recrystallization. Tabulae are flat or concave, sometimes incomplete, twelve to twenty-five in 5 mm.

Subfamily CATENIPORINAE Hamada 1957

Genus QUEPORA Sinclair 1955

Diagnosis. Cateniporinae with normal series of corallites, but without septal spinules.

Quepora bellensis sp. nov.

Plate 45, figs. 1–3

Holotype. USGD 11209, loc. 285; portion 5 (centre), parish of Mumbil, county of Wellington. Topmost Ordovician or Lower Silurian. Associated with *Palaeophyllum rugosum*.

Diagnosis. *Quepora* with small radiating corallum; fenestrules small, polygonal, smooth-

EXPLANATION OF PLATE 45

Figs. 1–3. *Quepora bellensis* sp. nov. 1, Transv. sect. of holotype USGD 11209. Note that the walls separating corallites are darker than the lateral walls; this is due to their structure, not to the presence of microcorallites. Loc. 285. $\times 4.0$. 2, Enlargement of palisade junction, middle right of fig. 1, showing structure; note the way in which an extension of the upper right corallite pseudo-morphs a microcorallite at the junction. The lack of microcorallites between the corallites is also shown. $\times 14.1$. 3, Longit. and oblique sect. of holotype USGD 11209, showing similar structures to fig. 2. $\times 4.0$.

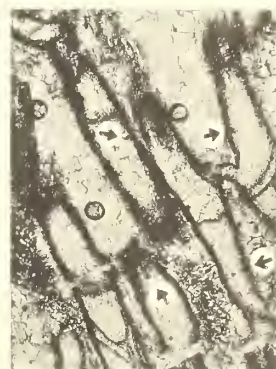
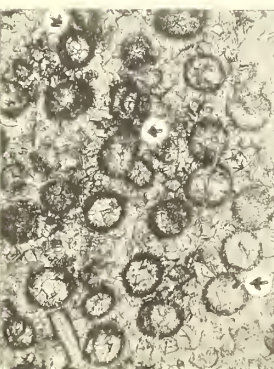
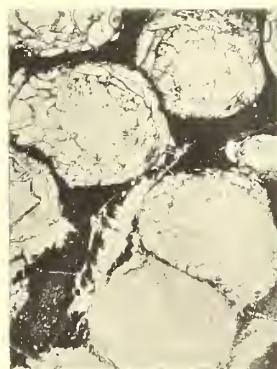
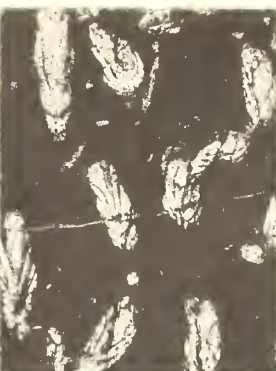
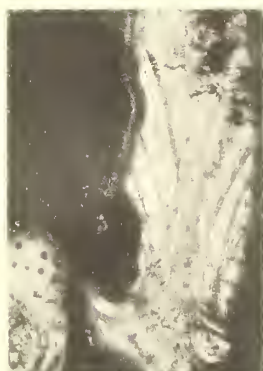
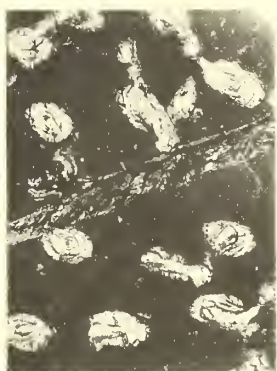
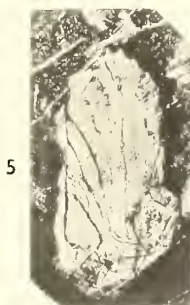
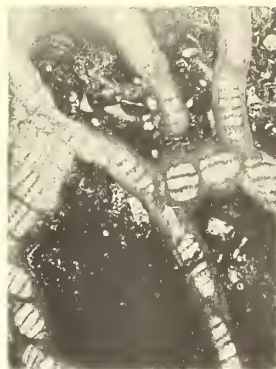
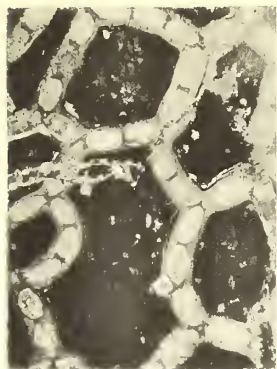
Figs. 4, 5. *Syringopora* sp. Transv. and longit. sects. of USGD 10175. Loc. 65. 4, $\times 3.6$; 5, $\times 6.6$.

Figs. 6–8. *Syringopora* sp. Transv. and longit. sects. of USGD 11107. Loc. 247. 6, $\times 3.6$; 7, $\times 14.5$, 8, $\times 5$.

Fig. 9. *Nipponophyllum multiseptatum* sp. nov. Transv. sect. of USGD 11099, holotype, $\times 1.8$.

Figs. 10, 11. *Syringopora* sp. Transv. and longit. sects. of USGD 11193. Arrows point to septa. 10, $\times 9.9$; 11, $\times 11.7$. Loc. 277.

Fig. 12. *Nipponophyllum* sp. aff. *giganteum* Sugiyama. Transv. sect. of USGD 10289. Loc. 208. $\times 2.1$.



sided; palisades of one to four oval corallites 1.0 to 1.5 mm. by 0.75 to 1.0 mm., with thick walls; tabulae close.

Description. The fenestrules are small, generally less than 5 mm. across, and polygonal, very rarely irregular. The palisades are straight or gently curved, with smooth or but faintly ribbed sides; they contain from one to four corallites. The corallites are oval, 1.0 to 1.5 mm. long (average about 1.2 mm.) and 1.0 mm. wide (including walls). The walls are thick, up to 0.2 mm., and are not waisted between corallites. There are no septa. Tabulae are flat, twelve to twenty in 5 mm. Very small round tubules occur at about 5 per cent. of the palisade junctions. However, at a couple of junctions one corallite can be seen to protrude between the other two, with a narrow neck almost cutting off this extension. It is probable that the tubules are formed in this way, and so it is doubtful that they can be true microcorallites. No microcorallites are visible between corallites.

Remarks. Differs from *F. chillagoensis* in the smaller regular fenestrules, the less elongate corallites, and the lack of septa.

Family AULOPORIDAE Edwards and Haime 1851

Subfamily SYRINGOPORINAE Nicholson 1879

Genus SYRINGOPORA Goldfuss 1826

Type species Syringopora ramulosa Goldfuss 1826.

Syringopora sp.

Plate 45, figs. 4, 5

Material. USGD 10175 (Pl. 45, figs. 4, 5), loc. 59; USGD 10191, loc. 65. Middle Silurian.

Description. All specimens collected are fragmentary, and so the corallum form is unknown. The corallites appear to be loosely connected, stolons being infrequent; they are 2 to 3 mm. in diameter, with thick walls. No septal spines are present, although the heavy recrystallization could obscure any. The tabulae are very closely set, and deeply inosculating. They do not form an axial tube, and frequently do not cross the tabularium, adhering cyst-like to one wall.

Syringopora sp.

Plate 45, figs. 6–8

Material. USGD 11107 (Pl. 45, figs. 6–8), 11108, loc. 247. Topmost Ordovician or Lower Silurian.

Description. Slightly radiating phaceloid corallum; the fairly regular cylindrical corallites are 1.0 to 1.5 mm. in diameter, the majority being 1.5 mm.; corallite walls thin. Connecting stolons frequent, $\frac{1}{4}$ to $\frac{1}{2}$ mm. in diameter. Septal spines long (0.25 mm.), thin, directed slightly upwards, and piercing the tabulae; they are fairly regularly placed, in twelve vertical rows, four in 1 mm. The tabulae are strong, deeply inosculating, coalescing to form an axial tube 0.25 mm. or more in diameter; they sometimes extend into the stolons.

Syringopora sp.

Plate 45, figs. 10, 11

Material. USGD 11193, loc. 277. Middle Silurian.

Description. Phaceloid; the corallites are cylindrical, 0.4 to 0.7 mm. in diameter (average 0.5 mm.), and closely set, the maximum separation being 0.7 mm., the average 0.25 mm. The corallite walls are thin or slightly thickened. Stolons are short, narrow, without tabulae, and occasionally bend upwards, forming a new corallite. Septal spines are not very common; they are short and blunt. Tabulae are irregularly spaced, 0.1 to 2 mm. apart, and thin; they may be flat and horizontal or oblique, gently sagging, or infundibuliform—usually excentrally. Rarely are they domed.

Remarks. The irregular, and often distant, spacing of the tabulae, and their frequent flatness, differs from the normal appearance of *Syringopora*. This species differs from *Eofletcheria* only in the presence of septa.

LOCALITY LIST

In New South Wales the major divisions are counties. These in turn are divided into parishes, usually of some 20 to 30 square miles, in which land has been sold as subdivisions of varying size, called portions. These are usually rectangular, and were mapped, using magnetic north, in the late nineteenth century. Apart from these parish maps, and aerial photos, no large-scale maps exist for large portions of western New South Wales, and so localities must be given in terms of these subdivisions. In the following list, all the localities except loc. 224 are in the Parish of Mumbil, County Wellington; por. = portion.

A. UPPER ORDOVICIAN OR LOWER SILURIAN

- Loc. 120 Por. 5; in gully, south side of boundary between pors. 5 & 93, & 850 yds. west of por. 96.
- 122 Por. 5; 500 yds. south of por. 93, & 620 yds. west of por. 96.
- 208 Por. 5; 550 yds. east of por. 3, & 1,200 yds. north of Mumbil-Neurea road.
- 247 Boundary between pors. 5 & 93, & 700 yds. east of por. 3.
- 257 Por. 126; 50 yds. east of Neurea-Dripstone road, & 480 yds. north of por. 125.
- 271 Por. 93; 80 yds. north-east of loc. 120, in same lens.
- 285 Por. 5; 850 yds. west of por. 108, & 780 yds. south of por. 93; same horizon as loc. 122.

B. TOPMOST LOWER, OR BASAL MIDDLE SILURIAN

- Loc. 59 Por. 93; 80 yds. south of por. 92, & 1,050 yds. east of por. 94.
- 65 Por. 93; 200 yds. south of por. 92, & 1,100 yds. east of por. 95.
- 71 Por. 5; 550 yds. east of por. 3, & 1,070 yds. north of Mumbil-Neurea road.

C. MIDDLE SILURIAN

- Loc. 1 'Mumbil' farmhouse; on Mumbil-Neurea road, south-west corner of por. 5.
- 26 Por. 5; 230 yds. south-south-east of 'Barnby Hills' homestead, & 670 yds. west of boundary between pors. 145 & 108.
- 33 Por. 3; 100 yds. west of por. 5, and 650 yds. north of Mumbil-Neurea road.
- 41 Por. 3; in gully, 20 yds. west of por. 5, & 480 yds. north of Mumbil-Neurea road.
- 58 Por. 92; 270 yds. north of por. 93, & 380 yds. west of railway line.
- 73 Por. 5; 650 yds. south of por. 93, & 400 yds. west of por. 108.
- 180 Por. 3; 250 yds. west of por. 5, & 1,250 yds. south of por. 95.
- 198 Por. 5; 600 yds. east of por. 3, & 1,150 yds. south of por. 93.
- 224 Por. 141, Parish of Narragal, County Gordon; 330 yds. north of por. 105, & 330 yds. west of Bell River.
- 229 Boundary between pors. 116 & 194, & 500 yds. west of Neurea-Dripstone road.
- 259 Por. 5; 250 yds. north-east from Mumbil-Neurea road, along drive to 'Barnby Hills' homestead.
- 276 Por. 89; 50 yds. south of boundary between pors. 89, 181, & 194.
- 277 Boundary between pors. 116 & 194, & 450 yds. west of Neurea-Dripstone road.
- 280 Por. 116; 50 yds. south of por. 194, & 500 yds. west of Neurea-Dripstone road.
- 284 Por. 5; 700 yds. west of por. 108, & 750 yds. south of por. 93.

D. UPPER SILURIAN

- Loc. 62 Limestone lens 20 yds. east of Mumbil-Neurea road, just north of turnoff to Baker's Swamp; south-west corner, por. 6.
 260 Limestone lens just above *M. bohemicus* horizon, por. 5; 450 yds. west of por. 145, & 600 yds. north-east of Mumbil-Neurea road.

E. SILURO-DEVONIAN

- Loc. 81 Por. 6; 300 yds. south of por. 141, & 700 yds. west of por. 138.

F. LOWER DEVONIAN

- Loc. 22 Boundary between pors. 68 & 123, on Mumbil-Dripstone road.
 63 Hillside, west side of Mumbil-Neurea road, boundary pors. 6 & 138.
 222 Mumbil-Dripstone road, 160 yds. west of turn off north to the 'Nindethana' tree nursery; por. 123.

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AUSTRALASIAN TYPHINAE (GASTROPODA) WITH NOTES ON THE SUBFAMILY

by PAUL VELLA

ABSTRACT. The Typhinae are a rare but widely distributed Muricid group. Because of their rarity they are of little value for local geological correlation, but are useful for regional correlation and palaeogeography, and as facies indicators.

Tertiary distributions indicate distinct American and Australo-European provinces and probably a third, Javanese province. The modern American fauna remains distinct. The single living European species is related to a living species on the west coast of South and Central America. *Typhina* and *Siphonochelus* each have closely related species living in Australia, New Zealand, the Indo-Pacific, the South Atlantic, and the Caribbean, showing a remarkable parallelism in their distribution, and are believed to have radiated simultaneously from Australia.

Two New Zealand species are members of a Tertiary endemic lineage. The remaining ten are not closely related to one another. Four are certainly related to distant overseas groups of similar age; five are possibly related to overseas groups of similar age; one is not closely related to any other known species.

The superspecific classification proposed by Keen (1944) is modified, her groups being redefined in terms of varix types. The new genus *Rugotyphis* and the new subgenus *Neotyphis* are described. The following genera and subgenera are recognized in Australia and New Zealand: *Typhis* (subgenera *Typhis*, *Hirtotyphis*, *Neotyphis*), *Rugotyphis*, *Typhina* (subgenus *Typhina*), *Siphonochelus*, *Lyrotyphis*, *Semityphis*. A check list of Australasian species with revised generic groupings is given. Twelve New Zealand species (eight new) and four Australian species are described.

INTRODUCTION

PREVIOUSLY only four species of Typhinae were recognized in New Zealand, and all were described under the general name *Typhis*. Fourteen species have been described from Australia. Iredale recognized the genera *Typhis*, *Typhina*, and *Siphonochelus*. He erected the subgenus *Choreotyphis* within *Typhina* but this has since been synonymized by Keen (1944) with *Siphonochelus*. Keen (1944, p. 56) allocated three New Zealand and six Australian species to *Typhinellus*. *Typhinellus*, however, is not recognized by the present writer, and the species placed in it by Keen are grouped below in *Typhis*, *Typhina*, and the new genus *Rugotyphis*. The genera and subgenera *Typhis*, *Hirtotyphis*, *Neotyphis*, *Typhina*, *Rugotyphis*, and *Siphonochelus* occur in New Zealand; *Typhis*, *Typhina*, *Siphonochelus*, *Lyrotyphis*, and possibly *Semityphis* occur in Australia.

Eight Tertiary and Recent new species from New Zealand are described below, bringing the New Zealand total to twelve. These with the Australian species make up a large proportion (about 30%) of all the species ascribed to the subfamily, and provide significant information relevant to phylogeny and classification.

Living and fossil Typhinae are rare. It must be assumed that present known ranges are generally less than true ranges and this must be taken into account when occurrences of Typhinae are used as evidence for Tertiary correlations or for faunal migrations. This is shown particularly well by the records of *Hirtotyphis* from antipodal areas, but from no intermediate localities, and by the odd space-time distribution of *Lyrotyphis*.

Ecology. Keen (1944, p. 51) noted that most Typhinae live in the neritic zone, almost all having been recorded from dredgings between 12 and 800 metres, averaging 50 metres.

Genus. Subgenus:		EOCENE		OLIG.		MIOCENE		PLIOC.	PLEIST.	RECENT.
		low	mid	up	low	up	low	mid	up	
TYPHIS		X	X	X						
	TYPHIS s.s.	X	X	X		?				X
	Europe	X	X	X						
	Australia					X				
	New Zealand			X	X	X	X			
	HIRTOTYPHIS					?		X	X	
	Europe							X	X	
	New Zealand					X		X		
	NEOTYPHIS							?	?	
	America									
	New Zealand							X		
TYPHINA										
	TYPHINA s.s.			?			X			X
	America									X
	Australasia						X			X
	S. Atlantic & W. Pacific									X
	TYPHINELLUS				?			X		X
	Europe									X
	Central America							X		X
RUGOTYPHIS										
	RUGOTYPHIS s.s.						X			
	New Zealand									
	c.f. RUGOTYPHIS						X	X	X	
	America									
TYPHISOPSIS										
	TYPHISOPSIS s.s.									X
	America									X
	TALITYPHIS						X			X
	America									X
	c.f. TYPHISOPSIS							X		
	Europe									
PTEROTYPHIS										
	PTEROTYPHIS s.s.									X
	America									X
	TRIPTEROTYPHIS						X			
	Europe									X
	America									X
LAEVITYPHIS										
	LAEVITYPHIS s.s.	X	X	X				?		
	Europe	X	X	X						
	America		X	X						X
	E. Africa									
	INDOTYPHIS			X				X		
	Java									
SIPHONOCHELUS										
	Europe									
	Australasia & W. Pacific					X		X	X	X
SEMITYPHIS										
	Java			X						
	Australia							X		
LYROTYPHIS										
	Europe									X
	Australia									

TEXT-FIG. 1. Stratigraphic and geographic distributions of the genera of Typhinae.

New Zealand Tertiary occurrences are all in very similar rocks—massive to poorly bedded, blue-grey calcareous siltstones, with rich molluscan faunas. These sediments were probably deposited in moderately deep to deep water (50–200 metres) on the continental shelf.

Modern Typhinae occur only in tropical or warm temperate seas. The New Zealand Recent species *Typhina pauperis* and *Siphonochelus solus* are extremely rare and confined to the northern (Aupourian) faunal province. Hence New Zealand's warmest waters must be close to the lower temperature limit.

DISTRIBUTION

Typhinae have been described from Tertiary rocks in southern and central Europe, the United States, the West Indies, Panama, Peru, Australia, New Zealand, Java, and India (a single Pliocene species). Australasian faunas more closely resemble European faunas than those of America or Java. The American faunas are difficult to interpret from literature, because of their difference from southern faunas, but they appear to be largely endemic with some relationships to New Zealand and European faunas. The Japanese fauna is essentially endemic.

Siphonochelus and *Typhina* are the only widely distributed living genera of the subfamily and are particularly interesting because they have the same distribution. Other living genera, even *Typhis* which was widespread in the Tertiary, are now restricted to small areas.

Many Typhine genera seem to have been able to disperse rapidly and to cross deep oceanic basins relatively freely. The mechanism by which they accomplished this is not known. Neither the larva nor the mode of life of the adults has been studied. The protoconch is paucispiral with a large nucleus and suggests that the larval stage has a short life. The relationship of present distributions of *Siphonochelus* and *Typhina* to existing ocean currents, however, shows that these genera almost certainly migrated in the currents. This implies, in spite of the protoconch, that the larval stage has a relatively long life.

The stratigraphic and geographic distribution of all the genera are summarized in the accompanying chart, text-fig. 1.

Tertiary distributions. Distributions and inferred migration directions of Eocene to Miocene Typhinae are summarized in text-figs. 3a and 3b.

During the Eocene (3b) distinct faunas occurred in Europe, America, and Java. The American fauna extended into Europe, but the European fauna did not reach America. The Java fauna of two essentially endemic genera remained distinct through most of the Tertiary and was probably confined to tropical water.

During the Oligocene and Miocene (3a) European genera spread to Australia and New Zealand. Most American genera were endemic, but some were related to New Zealand genera. Two European Miocene forms belong to a predominantly American group.

The persistence of a distinct fauna in Java and the lack of Typhinae in the Tertiary of Japan make it reasonably certain that migrations between New Zealand and America took place not around the Pacific margin, but directly across the central Pacific. Migration routes between America and Europe necessarily include many thousands of miles of deep ocean. It is assumed that most migrations of Typhinae resulted from the transport of larval stages in ocean currents.

From the order of appearance of groups in different areas, and from phylogenetic relationships, all migrations appear to have been eastward as shown in text-fig. 2, except for that of *Indotyphis* which is thought to have migrated to Java from America. Main migrations are believed to have taken place: (1) across the Atlantic from America to Europe; (2) through a Tethyan route, i.e. through the Mediterranean and northern Indian Ocean from Europe to Australia and New Zealand; (3) across the Pacific from New Zealand to America.

Distribution of living genera. Recent distributions are better known than those of the past and can be related directly to existing currents. Since Typhinae are confined to relatively warm waters, only warm ocean currents need be considered as possible aids to migration.

Restricted groups are:

1. The American group of related genera with wide flange-like varices extending across the shoulder, *Typhisopsis*, *Talityphis*, *Pterotyphis*, *Tripterotyphis*.
2. Two tiny species from off the west coast of Africa, referred to the once widespread genus *Laevityphis*, but possibly requiring a new generic name.
3. Two species of *Typhis s.s.* now confined to the New South Wales coast.

Three forms are widespread: *Typhina*, its subgenus *Typhinellus*, and *Siphonochelus*. *Typhina* and *Siphonochelus* have remarkably similar distribution, both occurring in Australia, New Zealand, the north-west Pacific, and the south Atlantic (text-figs. 2a, 2b). The living species of each are more closely related to one another than to any Tertiary forerunners.

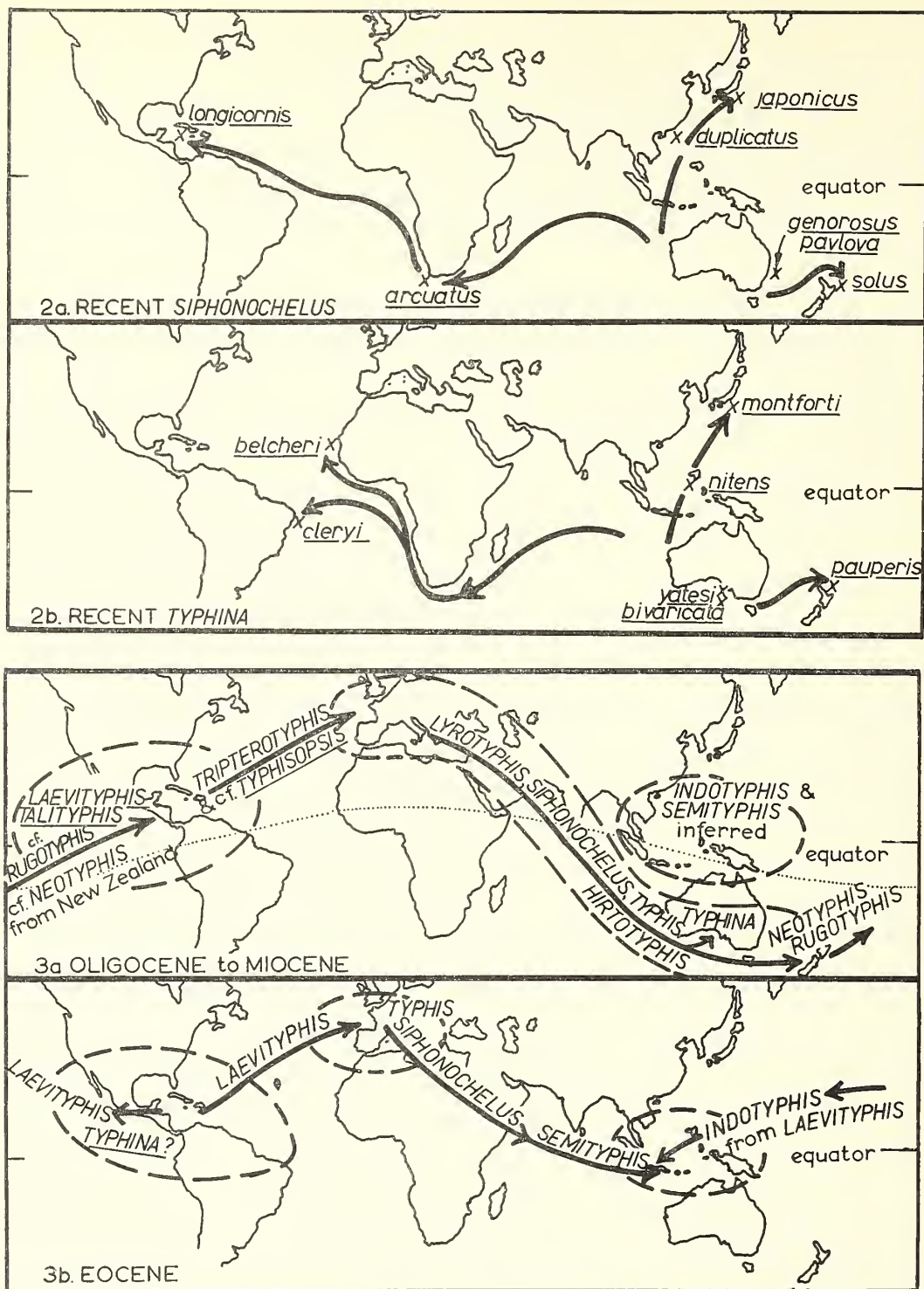
Siphonochelus became extinct in Europe after the Pliocene. It occurs in the Miocene and Pliocene of Australia, and now lives in New Zealand, Australia (two species), Japan, China Seas, South Africa, and Cuba. Though several Typhinae occur in the richly fossiliferous Tertiary rocks of Panama, the West Indies, and the United States, *Siphonochelus* has not been recorded as a fossil in America, and the Cuban species *Siphonochelus longicornis* (Dall) must be regarded as a recent invader.

The fossil record of *Typhina* is very incomplete. *Typhina dentata* (Johnson) from the Upper Eocene (Jackson) of the United States may not be a true Typhinae. The only reasonably certain fossil species are *T. laciniata* (Tate) and *T. disjuncta* (Tate) from the Lower Miocene (Balcomian) of Australia, and *T. tetragoniatus* (Cossmann) from the Pliocene of India. Living species have been reported from New Zealand, Australia (two species), Straits of Macassar (Borneo), Japan, Brazil, and north-west Africa. Australia was probably the source from which other areas were colonized (text-figs. 2a and 2b).

Each genus appears to have migrated along three routes, two of which correspond to existing ocean currents: (1) northward along the western Pacific margin, (2) eastward via the Tasman Current to New Zealand, (3) westward via the Equatorial Current in the Indian Ocean, around Cape of Good Hope, northward in the Benguela Current along the west coast of Africa, and finally north-westward in the Atlantic South Equatorial Current to Brazil (*Typhina*) and to Cuba (*Siphonochelus*).

Fleming (1957, pp. 19–22) in a discussion of the genus *Pecten* suggested that Pleistocene cooling would prolong larval stages and account for the known Pleistocene migrations. Migrations of *Typhina* and *Siphonochelus* probably also took place during the Pleistocene and could be explained in this way.

Tertiary migrations were on a smaller scale, but might similarly have depended on geologically more or less brief periods of favourable conditions.



TEXT-FIGS. 2, 3. 2, Distributions and inferred migration routes of (2a) *Siphonochelus*, (2b) *Typhina*; migration routes correspond to existing warm ocean currents. 3, Distribution and inferred migration routes of typhine genera during (3a) Oligocene to Miocene, (3b) Eocene; dashed lines delineate fossils; square brackets indicate geographic restriction. Dotted line in 3a indicates possible Miocene equator, after Koppen and Wegener 1924.

Typhinellus is represented by two living species, *T. sowerbyi* (Broderip) in the Mediterranean and *T. quadratus* (Hinds) on the Ecuador and Panama coasts. It is known as a fossil in the Pliocene of Italy, is possibly present in the Oligocene, and probably originated in Europe. *Typhinellus* must have migrated across the Atlantic before the emergence of the Isthmus of Panama near the end of the Pliocene (Dunbar 1949, pp. 491–2).

STRATIGRAPHIC USE

Local correlation. New Zealand Tertiary Typhinae are rare and have little value for internal correlation. Of the ten species known, nine are from single localities or local districts, and one, *Typhis* (*Neotyphis*) *tepungai* Fleming, from several localities in the south of the North Island.

Regional correlation. New Zealand species from at least three stratigraphic levels are more closely related to overseas species of similar age than to earlier New Zealand species.

(1) Lower–Middle Oligocene: *Typhis* (*Typhis*) *adventus* sp. nov. is closely related to the Australian Oligocene *T. (Typhis) maccoyi* Tenison-Woods, and to the European lower Tertiary type species, *T. (T.) tubifer* (Brug.).

(2) Upper Miocene: *Typhis* (*Hirtotyphis*) *aoteanus* sp. nov. is related to *T. (H.) horridus* (Brocchi), widely distributed in the upper Miocene and Pliocene of Europe.

(3) Recent: the genera *Typhina* and *Siphonochelus* have no known Tertiary representatives in New Zealand. The Recent species *Typhina* (*Typhina*) *pauperis* (Mestayer) and *Siphonochelus solus* sp. nov. have affinities with Recent species in Australia and elsewhere, as explained above.

Several less definite overseas correlations are suggested by Typhinae. The Lower Miocene *Typhis* (*Typhis*) *clifdenensis* sp. nov., *T. (Hirtotyphis) aculeatus* sp. nov., *Rugotyphis francescae* (Finlay), and the Pliocene *T. (Neotyphis) tepungai* Fleming, have no known closely related ancestors in New Zealand. *Rugotyphis* and *Neotyphis* are possibly represented by species in the Miocene of Central and North America. No known overseas species of *Typhis* is close to *clifdenensis*. A possible relative of *T. (Hirtotyphis) aculeatus* in the Miocene of Italy is discussed in the systematic section below.

Stratigraphic ranges of New Zealand and Australian species are given in the check list on p. 379.

CLASSIFICATION

In 1880 Jousseaume subdivided the genus *Typhis* by introducing twelve new generic names. Of these nine are now in use, though some are reduced to subgeneric rank. For more than sixty years, however, most of Jousseaume's names were neglected and the remainder were largely misapplied. Authors dealing with local faunas usually described species under one of the group names *Typhis*, *Siphonochelus*, and *Typhina*, and both Cossmann (1903) and Thiele (1931) synonymized many of Jousseaume's valid groups. Jousseaume's work received due credit for the first time in the revision by Keen (1944).

Keen's catalogue of species and bibliography greatly facilitate study. Her generic revision, though a great step forward, was yet too conservative. Keen's phylogenetic account and subgeneric groupings are based mainly on the number of varices per whorl, and the position of the intervariceal tubes relative to the varices. Other important features are neglected.

The number of growth steps per whorl, the position and inclination of the intervariceal tubes, and the form of the varices, protoconch, aperture, and anterior canal are useful conservative shell features that are discussed below.

Growth steps. Each varix (sometimes paired) terminates a growth step. Of nine genera of Typhinae, six have 4·2 growth steps per whorl, and these include such distinct groups as *Typhis*, *Siphonochelus*, *Laevityphis*, and *Talityphis*. The number of growth steps per whorl is constant from juvenile to adult. It follows that 4·2 growth steps per whorl is a fundamental character of the subfamily, presumably inherited from a pre-Eocene common ancestor. Various groups with 4·2 growth steps per whorl, distinguishable mainly by variceal characters, evolved, in most cases prior to the Eocene, and some of these subsequently gave rise to the divergent groups with three or five growth steps. Two genera have three growth steps per whorl and one has five, and these can be related by the forms of their varices to groups with the standard 4·2 growth steps.

Aperture and anterior canal. The aperture and anterior canal are so conservative that they are only exceptionally of use for generic classification. Typically the aperture is entire, broadly ovate or circular, surrounded by a thin, raised rim which rarely is in part expanded to form a secondary varix; the lower border may be rounded, or faintly angled in accordance with the angle at which the outer and inner walls of the final growth stage are united. The only exception is the aperture of *Lyrotyphis*.

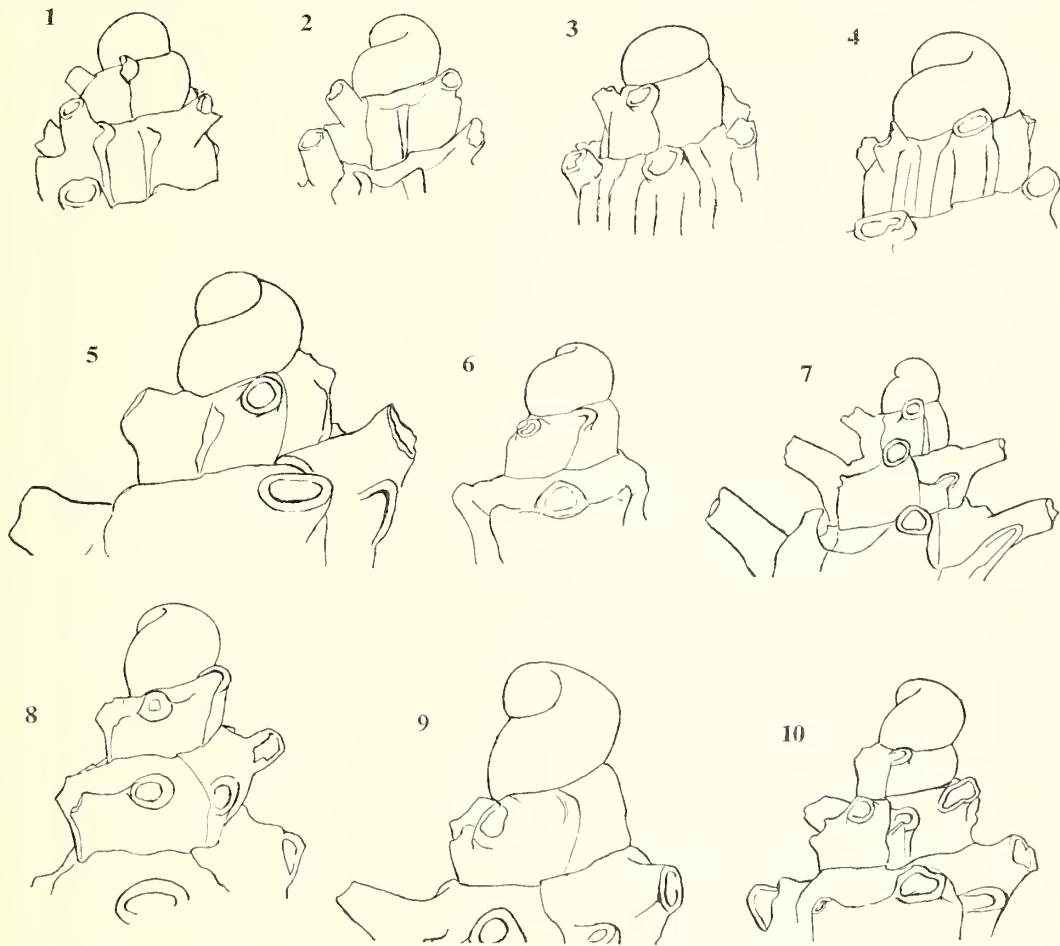
The anterior canal is always closed, typically broad and flattened, carrying the lower part of the varix, and bent more or less sharply to the right, tapering in well-preserved specimens to a delicate subcylindrical tube. Canals of the previous growth steps forming the body whorl are visible, and distinct from the final canal and from one another. *Haustellotyphis* is exceptional in having a straight canal without distinct earlier canals.

Intervariceal tubes. In all specimens examined the intervariceal tubes have approximately the same position on the growth steps. All the shells have linear ridges or scars indicating the positions of former apertures, and the tubes arise on the shoulder directly in front of these. The tubes are usually about mid-way between the varices, but their position relative to the varices depends on the position of the varices on the growth steps. *Typhinellus sowerbyi* has secondary varices developed on the apertural rim, and consequently Keen was correct in stating that the tubes are 'nearer to preceding than to succeeding varices'. Some species of *Typhina*, however, which are supposed to have tubes mid-way between the varices, also have secondary varices on the apertural rim, and just behind the tubes on earlier growth steps. In both *Typhinellus* and *Typhina* the tubes are mid-way between the primary varices, and other characters must be used to distinguish these forms. The position of the intervariceal tubes seems to have no value except for distinguishing a few overseas groups.

In some groups the inclination of the intervariceal tubes is significant. In *Typhis s.s.* the tubes consistently point obliquely backwards and usually only slightly above the horizontal. The most divergent species is *Typhis clifdenensis* in which the tubes are twisted upwards at an exceptionally high angle ($c 40^\circ$) from the horizontal. The backward deflection of the tubes is constant in *Typhis s.s.* and persists in the subgenera *Hirtotyphis* and *Neotyphis*. In *Rugotyphis*, on the other hand, the tubes are nearly radial and confirm that this genus is divergent from *Typhis*. In *Laevityphis*, *Siphonochelus*, and

Lyrotyphis the tubes point almost vertically upward, sometimes a little backward. The adult shell of *Neotyphis* is convergent to *Laevityphis* in the characters of the tubes and varices, but the juvenile characters show it to be related to *Typhis*.

Protoconch. In describing protoconchs the term nucleus is used as recommended by



TEXT-FIG. 4. Apices of Typhinidae: 1, 2, *Typhina* (*Typhina*) *bivariata* (Verco); 3, 4, *Lyrotyphis* *syringianus* (Hedley). 5, *Typhina* (*Typhina*) *yatesi* (C. & F.). 6, *Typhis* (*Typhis*) *hebetatus* Hutton. 7, *Typhina* (*Typhina*) *pauperis* (Mest.). 8, *Typhis* (*Typhis*) *adventus* sp. nov. 9, *Typhis* (*Neotyphis*) *tepingai* Fleming. 10, *Typhis* (*Typhis*) *maccoyi* Ten.-Woods.

Marwick (1957, p. 14) for the 'semiglobular initial part' consisting of about half a whorl. Protoconch whorls were counted as proposed by Burnett Smith (1945).

Protoconchs are lacking from most New Zealand specimens and are not known for *Hirtotyphis*, *Rugotyphis*, and *Siphonochelus*. Protoconchs have been available on *Neotyphis tepungai*, *Lyrotyphis syringianus*, and three species each of *Typhis* s.s. and *Typhina* s.s., all of which are illustrated in text-fig. 4.

In both *Typhis* and *Typhina* the protoconchs have a consistent form, and between

each group are consistent differences. *Typhis* has a tall protoconch of one and a half to one and three-quarter whorls, commencing with a large rounded eccentric nucleus. From the nucleus the initial whorl rapidly expands to full diameter so that the protoconch is subcylindrical. *Typhina* has a protoconch of about one and a quarter whorls, with an eccentric nucleus similar to that of *Typhis*, but expanding more gradually so that the lower part is considerably broader than the top.

Only one slightly worn protoconch of *Neotyphis* is known. Except that it seems to have an incipient peripheral angle, it is similar to that of *Typhis*. The protoconch of *Lyrotyphis* differs from that of *Typhina* only in having a more depressed initial whorl.

Protoconchs have systematic value but few useful descriptions have been published.

Types of varices. Six varix types are recognized. At least three have existed since the Eocene. Varix types are regarded as more fundamental to classification than the number of growth steps per whorl, and in the classification proposed below each varix type distinguishes a genus or a group of related genera. Forms with more or less than the standard 4·2 growth steps per whorl are given generic rank within their varix type group. Most subdivisions based on other characters are given subgeneric rank.

For convenience, each varix type is referred to by the name of the genus or most important genus of which it is characteristic. The six varix types are described below:

1. *Siphonochelus* type: smooth and rounded, not crossing the shoulder to the previous whorl, but curving back at the top to coalesce with the intervariceal tube. It is misleading to describe the tubes of *Siphonochelus* as immediately preceding the varices, because the tubes are situated just ahead of the scars of former apertures, and occupy the same relative position on the growth steps as in other genera. *Siphonochelus* has always been recognized by its distinctive varices. *Semityphis* with three growth steps per whorl, and *Lyrotyphis* with five growth steps per whorl, both have varices like those of *Siphonochelus*. As *Siphonochelus* has the fundamental 4·2 growth steps per whorl, it is considered to have evolved first, and *Lyrotyphis* and *Semityphis* are regarded as derivatives.

2. *Laevityphis* type: rounded folds not crossing the shoulder, each surmounted on top by a single, vertical hollow conical spine. The intervariceal tubes are nearly vertical. In the subgenus *Indotyphis* the tubes are differently disposed, and relationship is inferred solely from variceal characters.

3. *Typhis* type: broad, rounded folds not crossing the shoulder, each with hollow conical spines arranged in a linear series along the crest and diminishing downwards. In *Typhis s.s.* the varices and variceal spines curve backwards. In *Hirtotyphis* the spines become grotesquely enlarged, straight or nearly straight and radial. In *Neotyphis* all but the uppermost spine on each varix are obsolete and the uppermost spine points nearly vertically upward.

Typhis s.s., with typical varices, has persisted from the Lower Eocene to the Recent. The consistent backward deflexion of the intervariceal tubes, and the similarity of protoconchs, discussed above, are confirming evidence of the relationship of the forms grouped in *Typhis*.

4. *Typhina* type: thin, frilled flanges, with open trough-shaped spines contrasting with the closed, hollow, conical spines of *Typhis* and *Laevityphis*. The main varix does not cross the shoulder vertically, but runs forward along the peripheral angle of the whorl as a low flange, then curves upward to join the apertural rim at a tangent. In *T. belcheri*

and *bivaricata*, and in the two living species of *Typhinellus*, part of the apertural rim is expanded to form a secondary varix. In *T. pauperis* and *yatesi* the apertural lip is not expanded.

At the top of each primary varix a large trough-like spine curves upward and in toward the spire, usually with a slight twist either backward or forward. The outer edge of each varix may be produced to small trough-shaped spines at intervals below the upper spine, or may be simply frilled. In *Typhina* the outer edge of each varix curls forward; in *Typhinellus* it curls backward.

5. *Rugotyphis* type: intermediate between the *Typhis* type and the *Typhisopsis* type. It resembles the *Typhis* type in being broad at the base, fold-like and curved slightly but distinctly backwards. It resembles the *Typhisopsis* type in extending across the shoulder and having an acute foliated crest. Other distinctive features are an ornament of irregular, more or less radial ribs on the front face only, and tiny trough-shaped spines on the crest of the varix below the shoulder. The part of the varix crossing the shoulder is lower and narrower than the part below the peripheral angle, bears no spines, and runs obliquely forward toward the suture, abutting against the corresponding varix on the previous whorl. The varices thus form four continuous ridges ascending in steep sinistral spirals to the apex of the shell.

6. *Typhisopsis* type: elevated, flange-like, frilled, crossing the shoulder, extending with little change in elevation from the anterior canal to the previous whorl, characteristic of an American group which appeared in the Miocene and persists at the present day, comprising *Typhisopsis* and *Talityphis* each with 4.2 growth steps per whorl, and *Pterotyphis* and *Tripterotyphis* each with 3 growth steps per whorl.

Summary of classification based primarily on varix types.

The suggested reclassification of the Typhinae is set out in tabular form below. The asterisk (*) indicates subgenera not known in Australasia.

1. *Siphonochelus* group: varices broadly rounded, fold-like, typically without spines, curving back at the top to coalesce with the tubes.

Genera *Siphonochelus*: 4.2 growth steps per whorl.

Lyrotyphis: 5 growth steps per whorl.

Semityphis: 3 growth steps per whorl.

2. *Laevityphis* group: varices broadly rounded, fold-like, not crossing the shoulder, each surmounted on top by a single, nearly vertical spine.

Genus *Laevityphis*: 4.2 growth steps per whorl.

*Subgenus *Laevityphis*: tubes nearly vertical.

*Subgenus *Indotyphis*: 'tubes twisted forward and soldered to the back of the next varix' (Keen 1944, p. 52).

*Subgenus *Pilsbrytyphis*: irregular axial sculpture.

3. *Typhina* group: primary varices flange-like, excavated in front, inclined forward, each with a large, trough-like spine at the top, curving up and in toward the spire; not crossing the shoulder vertically, but running forward along the periphery as a low lamellar flap, then curving up to join the apertural rim. Secondary varices developed in some species by extension of the apertural rim.

Genus *Typhina*: 4.2 growth steps per whorl.

Subgenus *Typhina*: outer edge of varix curling forward; varix retracted at the top of the anterior canal, in some species represented on the canal by flattened, fin-like spines; body whorl more or less convex.

*Subgenus *Typhinellus*: outer edge of varix curling backwards; varix crossing without reduction in width from body to anterior canal; body whorl more or less regularly tapered.

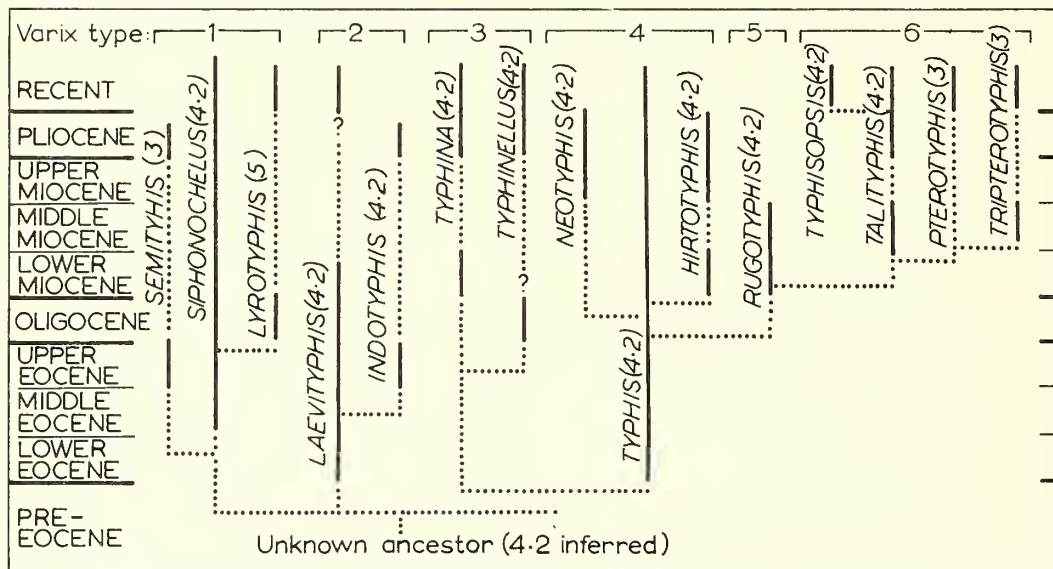
4. *Typhis* group: varices broad, rounded, fold-like, not crossing the shoulder, each bearing on the crest a row of hollow conical spines.

Genus *Typhis*: 4·2 growth steps per whorl.

Subgenus *Typhis*: varices of body whorl each with three to eight backward curving spines of moderate size; tubes bent obliquely backwards, and upwards not more than 40° from horizontal.

Subgenus *Hirtotyphis*: varices of body whorl each with three to six large, nearly straight, radial spines.

Subgenus *Neotyphis*: adult varices each with one nearly vertical spine on top, obsolete spines below; adult tubes nearly vertical; juvenile varices and tubes as in *Typhis*.



TEXT-FIG. 5. Phylogeny of the Typhinae; where possible names are written opposite epoch at which genera or subgenera make their first definite appearance; query (?) indicates species doubtfully referred to a genus or subgenus; dotted lines show where lineages are not represented by fossils; varices per whorl given by number in brackets above each name.

5. *Rugotyphis* group: varices extending across shoulder to previous whorl, ornamented on the front faces with irregular, more or less radial ribs, broad based, but with acute foliated crests serrated by tiny trough-shaped obsolete spines.

Genus *Rugotyphis*: 4·2 growth steps per whorl.

6. *Typhisopsis* group: varices elevated, flange-like, frilled, extending with little change in width from anterior canal to previous whorl.

Genus *Typhisopsis*: 4·2 growth steps per whorl.

*Subgenus *Typhisopsis*: tubes connected to previous whorls by laminar buttresses.

*Subgenus *Talityphis*: tubes free.

Genus *Pterotyphis*: 3 growth steps per whorl.

*Subgenus *Pterotyphis*: tubes free.

*Subgenus *Tripterotyphis*: tubes coalesced with succeeding varices.

PHYLOGENY

The relationships of the genera and subgenera are summarized in the phylogenetic table, text-fig. 5, and are discussed in the systematic descriptions below.

SYSTEMATIC DESCRIPTIONS OF THE GENERA

Descriptive terminology. 'Preceding varix' and 'succeeding varix', Keen (1944), mean previously formed varix and later formed varix.

The shell is considered to be oriented with the axis of coiling vertical, the apex pointing up and the aperture facing the observer. Top and bottom and similar words are applied in their absolute sense to the shell as oriented. Forward and backward mean toward and away from the aperture in the direction of coiling.

Synonymies. Full synonymies of the genera were given by Keen (1944) and are not repeated.

Genus TYPHIS Montfort 1810

Type species, by original designation, *Purpura tubifer* Bruguière 1792 (Eocene, Grignon, France).

Cossmann's figure (1903, pl. 2, fig. 23) of *Typhis tubifer* shows rather narrow, but rounded variceal folds, each bearing on the crest a linear series of tubular spines. The varices do not cross the shoulder, and the final one extends, gradually diminishing downwards, on to the anterior canal. According to Keen (1944, p. 53) Bruguière's original figure shows *tubifer* to have about twice as many variceal spines as *T. pungens* (Solander) (here figured Pl. 47, fig. 29), a British Eocene species which has three spines per varix. New Zealand species of *Typhis* s.s. invariably have six spines on each varix of the body whorl.

Each variceal spine bears on its front face a longitudinal, linear, sutural groove, extending from the tip on to the front surface of the varix. On well-preserved specimens the varix between each pair of sutural grooves is covered by arcuate growth-lines which are convex towards the aperture and meet the sutural grooves almost tangentially. A specimen of *T. hebetatus* Hutton from Awamoa (Pl. 46, fig. 13) has an incompletely formed final growth step on which the spines are trough-shaped, lamellar structures still open towards the front. It is clear that the sutural groove of the complete spine is the seam along which the two sides of the originally open trough-shaped spine are joined. On neanic whorls of all species of *Typhis* that have been examined the variceal spines are open trough-shaped structures.

On adult whorls of *Typhina* the single large variceal spine on each varix is typically a lamellar trough-shaped structure. The only known exception is the Australian *Typhina* (*Typhina*) *yatesi* (C. & F.) in which the spine is closed for part of its length, the sides of the trough having curled far enough around to meet and become soldered together. The neanic variceal spines of *Typhis* apparently recapitulate a stage in evolution comparable with the adult spines of *Typhina*. The latter was probably represented in the Eocene by *Typhis dentatus* Johnson (Jackson, Mississippi), referred to *Typhina* by Keen (1944, p. 66), and it is inferred that *Typhis* and *Typhina* evolved, as shown in text-fig. 3, from a hypothetical pre-Eocene ancestor close to *Typhina*.

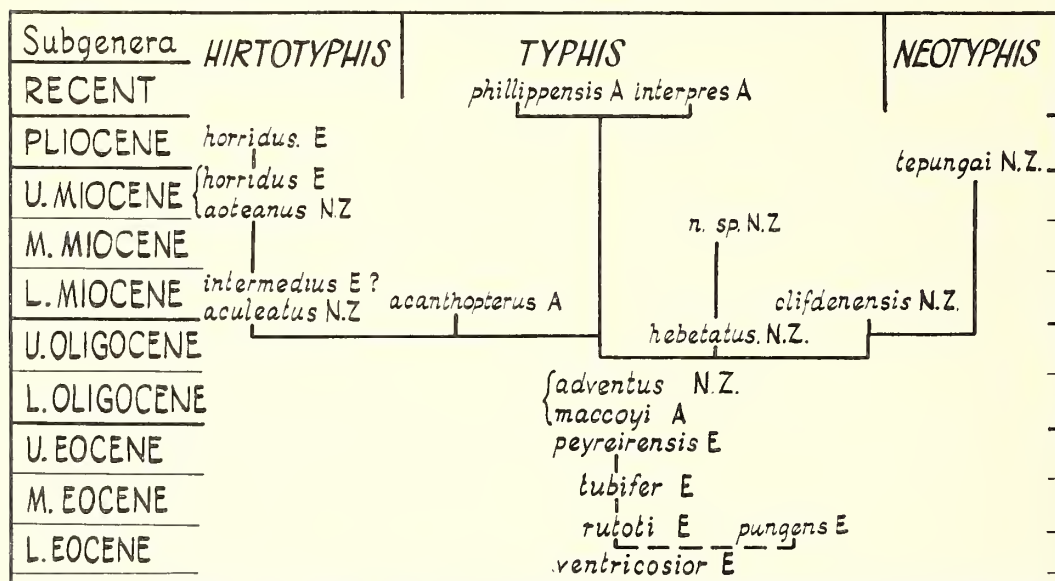
Typhina, *Typhinellus*, *Haustellotyphus*, *Talittyphis*, and *Typhisopsis*, all having 4·2 growth steps per whorl, and regarded by Keen as subgenera of *Typhis*, are here grouped in different genera. Three subgenera of *Typhis* are recognized:

<i>Typhis</i>	<i>sensu stricto</i>
<i>Hirtotyphis</i>	(regarded by Keen as synonymous with <i>Typhis</i>)
<i>Neotyphis</i>	new subgenus.

Hirtotyphis and *Neotyphis* are Miocene–Pliocene short-lived derivatives of *Typhis*,

represented by few species. The subgenus *Typhis* is a conservative group including six European, five New Zealand, and four Australian species, ranging in age from lower Eocene to Recent. The stratigraphic and geographic occurrences and probable phylogenetic relationships of species of *Typhis*, *Hirtotyphis*, and *Neotyphis* are summarized in text-fig. 6.

A description of the French Eocene *T. peyreirensis* Cossmann and Peyrot has not been seen. The Australian and New Zealand Oligocene species *T. maccayi* T.-Woods.



TEXT-FIG. 6. Phylogeny of Genus *Typhis*. Subgenera shown in upper-case italics, species in lower-case italics. E, Europe, A, Australia, NZ, New Zealand, indicate where species occur.

and *T. australis* sp. nov. are close to the European upper Eocene *T. tubifer* (type species of *Typhis*). Relationship of these three species to the European Oligocene *T. peyreirensis* is inferred but has not been confirmed. According to Keen (1944, p. 65) the Italian Lower Miocene *T. intermedius* was confused with *Hirtotyphis horridus* (Brocchi) by Montanaro (1934, p. 10, pl. 1, fig. 1). On account of its greatly enlarged upper variceal spines and obsolete lower spines the New Zealand Lower Miocene *Typhis* (*Hirtotyphis*) *aculeatus* is thought to belong to the same lineage as *Hirtotyphis aoteanus* and *horridus*. *T. intermedius* also belongs to this group. These four species are grouped in *Hirtotyphis* to emphasize this relationship but the earlier species *aculeatus* and probably the Italian form are less distinct from *Typhis* s.s. than are the later species.

The genetic relationships between species of *Typhis* and of *Hirtotyphis* suggested in text-fig. 6 imply communication between Europe and Australasia (or at least New Zealand) from about Middle Oligocene to Upper Miocene time. The Pliocene *Neotyphis*, on the other hand, has no European relatives, but it possibly has some representatives among Miocene and Pliocene American shells referred by Keen to *Laevityphis* (e.g. *L. linguiferous* (Dall)).

The double varices of the Australian Lower Miocene species *T. acanthopterus* Tate

are abnormal, but probably do not indicate a fundamental difference. A similar, though not parallel, modification is exhibited by some species of *Typhinellus* and *Typhina*, particularly by *Typhina* (*Typhina*) *bivaricatus* (Verco).

Subgenus HIRTOTYPHIS Jousseaume 1880

Type species, by original designation, *Hirtotyphis horridus* (Brocchi) = *Murex horridus* Brocchi 1814, Upper Miocene–Pliocene, Europe.

Hirtotyphis horridus is distinguished by three very large, nearly straight, radially directed spines on each varix of the body whorl. The discovery of related species in Miocene rocks of New Zealand lends greater significance to the form which is widely divergent from the New Zealand Miocene and Australian Recent species of *Typhis* s.s.

Subgenus NEOTYPHIS subgen. nov.

Type species *Typhis tepunga* Fleming 1943, Pliocene, New Zealand.

Shell of moderate size with 4·2 growth steps per whorl, varices rounded folds, not crossing the shoulder, nearly smooth except for a single vertical spine on top of each—simulating *Laevityphis*; tubes midway between varices, directed obliquely backwards, steeply upwards on adult whorls but almost horizontally on the first post-nuclear whorl; neanic varices as in *Typhis* s.s.; protoconch large, differing from that of *Typhis* s.s. in having an incipient peripheral keel.

Remarks. Each varix of the body whorl of *Neotyphis tepungai* has two nodules on the crest at intervals below the vertical spine. On the holotype the upper nodule of the terminal varix is produced to a tiny hollow conical backward curving spine. The nodules are vestigial spines with sutural grooves. The growth-lines of the varices have the same relation to these as in *Typhis* s.s. *Neotyphis* is thus closely related to *Typhis*, not to the superficially similar *Laevityphis*. The neanic varices and tubes confirm this relationship.

Typhis linguiferus Dall, placed in *Laevityphis* by Keen, may be a *Neotyphis*. According to Dall (1890, p. 152, pl. 12, fig. 7) the protoconch has 'two laxly coiled, polished, peripherally-keeled nuclear whorls'. Judged from Dall's figure (Gardner 1947, p. 53, fig. 17) the peripheral keel is not obvious, and the protoconch is very like that of *Neotyphis tepungai*. *T. linguiferus* also resembles *Neotyphis* and not *Laevityphis* in the position of the varices relative to the tubes and in the nature of the neanic varices and tubes. On the other hand, Dall's figure shows no trace of vestigial spines on the varices. *T. linguiferus* is closer to *Neotyphis* than to *Laevityphis* and is tentatively included in *Neotyphis*.

Genus LAEVITYPHIS Cossmann 1903

Type species, by original designation, *Typhis coronarius* Deshayes 1865, Lower Eocene, France.

Laevityphis coronarius is a small, elongate shell with narrow, but rounded, smooth varices each with a single almost vertical spine on top. The terminal varix is well behind the aperture and earlier varices are closer to the preceding than to the succeeding tubes. Cossmann's illustration (1903, pl. 2, fig. 18) shows both tubes and spines nearly vertical on all (including neanic) whorls.

Laevityphis is mainly an Eocene–Oligocene group. Of the American Miocene species referred here, *Typhis cercadicus* Maury (from Santa Domingo) seems to be the only true

Laevityphis. *Typhis sawkinsi* Mansfield has varices extending across the shoulder and may be generically distinct. *T. costaricensis* was first described as a variety of *T. linguiferus* and may be a *Neotyphis*.

The East African Recent species *T. transcurrens* von Martens and *T. tubuliger* Thiele, referred to *Laevityphis* by Keen, are much smaller than Tertiary species and may be a distinct genus or subgenus.

Pilsbrytyphis Woodring 1959 is regarded as a subgenus of *Laevityphis*, differing in having irregular ornament.

Genus RUGOTYPHIS gen. nov.

Type species *Typhis francescae* Finlay 1924, Lower Miocene, New Zealand.

Shell large for the subfamily, solid, with 4.2 growth steps per whorl; tubes directed radially or only slightly backwards, nearly horizontal; varices about midway between tubes, broad, elevated, with acute, foliated, crenulated crests, inclined away from the aperture, continued across the shoulder and contiguous with varices of previous whorl, forming four steep, sinistral spiral ridges from body to apex; apertural sides of varices ornamented with irregular, more or less radial ribs; reverse sides of varices and remainder of shell smooth except for growth-lines; protoconch not seen.

Remarks. Superficially *Rugotyphis secundus* sp. nov. resembles *Typhis hebetatus* Hutt. but *Rugotyphis* differs from *Typhis* in the nearly radial tubes, the continuation of the varices over the shoulder, and the lack of conical spines on the varices. The part of the varix crossing the shoulder is narrower and less elevated than the portion below the peripheral angle and is not crenulated. The crenulations of the lower parts of the varices are formed by tiny lamellar spines which curl forward at the edges to become shallowly trough-shaped.

The size and shape of the shell and the solidness and backward inclination of the varices suggest that *Rugotyphis* is intermediate between *Typhis* and *Typhisopsis*.

Two American species may belong to *Rugotyphis*, *Typhis harrisi* Olsson (Florida, Miocene), and *T. floridanus* Dall (Florida, Pliocene). *T. floridanus* has varices extending across the shoulder, with oddly twisted spines on the peripheral angle. Dall (1889, p. 216) described the ornament on the front surface of the varix as follows: 'spiral sculpture of a few low ridges extending from the vicinity of the aperture to the summit of the varix, where they appear as serrations or abortive spines'. This description fits *Rugotyphis* much better than *Typhina* or *Typhinellus*.

Genus TYPHINA Jousseaume 1880

Type species, by original designation, *Typhis belcheri* Broderip 1833, Recent, off Cape Blanco, West Africa.

Typhina and *Typhinellus* are here grouped together as subgenera of the genus *Typhina*. Both names were first published in Jousseaume's summary list of the Muricidae (1880, p. 335). According to Iredale (1924, p. 272) *Typhinellus* appears ahead of *Typhina* in the list, and therefore has page precedence for generic status. The International Rules recommend that page precedence should be observed in the event of 'other things being equal'. *Typhina* is given generic status because it is the larger, more important, more widespread and apparently older group. *Typhinellus* is considered to be a specialized

derivative of *Typhina* and therefore is more appropriately regarded as a subgenus of *Typhina*.

Reeve's illustrations of *T. belcheri* (1842, pl. 240, figs. 5, 6) show clearly the structure of the varices. Photographs of Reeve's illustrations are reproduced below (Pl. 47, figs. 17, 18). Both primary and secondary varices are present. The outer edges of the primary varices are crenulated and curled forward. The secondary varices are simple low outgrowths of the apertural rim, extending from the previous whorl to opposite the peripheral angle. The intervariceal tubes are situated midway between the primary varices and are bent obliquely backwards and upwards at a moderate angle from the horizontal.

In the indisputable species of *Typhina*, *yatesi* and *pauperis*, secondary varices are not developed. In *T. bivaricata* the secondary varices are almost as large as the primary varices, the whole of the outer semicircle of the apertural rim being expanded to form a prominent variceal flange. In *Typhina*, therefore, the secondary varix is quite variable, and has no generic significance.

Subgenus TYPHINELLUS Jousseaume 1880

Type species, by original designation, *Typhis sowerbyi* Broderip 1883, Recent, Mediterranean.

That Knudsen (1956, pp. 20, 21) regarded *T. belcheri* as a synonym of *T. tetrapterus* of Kobelt 1887 (= *T. sowerbyi*) emphasizes the similarity between *Typhinellus* and *Typhina*. Separation of the two subgenera, however, is supported by their different space-time distributions.

T. sowerbyi is well illustrated by Reeve (1842, pl. 240, figs. 7, 8, 9), and his figures are reproduced (Pl. 47, figs. 14, 15, 19).

Three main characters distinguish *Typhinellus* from *Typhina*: (1) The outer edges of the primary varices of *Typhinellus* curve backward instead of forward as in *Typhina*. (2) The primary varices of *Typhinellus* continue without constriction on to the anterior canal, whereas those of *Typhina* are constricted at the top of the canal and in most species are absent from the canal or are represented by flat fin-like spines. (3) The body whorl of *Typhinellus* tapers almost regularly from the peripheral angle to the anterior canal; that of *Typhina* is generally strongly convex.

Typhinellus appears to have originated in Europe. The only undoubted fossil record is *T. tetrapterus* (Brown) from the Pliocene of Europe, regarded by Keen as a synonym of *T. sowerbyi*. A shell from the Oligocene of Italy was described by Sacco (1904, p. 17, pl. 4, fig. 20) as *Typhis (Typhinellus) tetrapterus* var. *protetrapterus*. The writer has not seen Sacco's description. If a true *Typhinellus*, this shell would show that *Typhinellus* has been distinct from *Typhina* for a much longer time than would seem likely from their relatively small differences.

The shell from the Miocene of Hungary, illustrated as *Murex (Typhis) tetrapterus* by Hoernes (1856, pl. 26, fig. 10), has varices continuing directly across the shoulder and lacking even the single spines of *Typhinellus*. It is not a *Typhinellus*, but seems to belong to the American *Typhisopsis* group and probably needs a new generic name.

A revised list of species of *Typhina* and *Typhinellus* is given below:

- Typhina (Typhina) belcheri* (Broderip), Recent, West Africa
- Typhina (Typhina) bivaricata* (Verco), Recent, South Australia
- Typhina (Typhina) cleryi* (Petit), Recent, Brazil
- Typhina (Typhina) disjuncta* (Tate), Miocene, Australia

Typhina (*Typhina*) *laciniata* (Tate), Miocene, Australia
Typhina (*Typhina*) *montforti* (A. Ad.), Recent, Japan
Typhina (*Typhina*) *nitens* (Hinds), Recent, Straits of Macassar
Typhina (*Typhina*) *pauperis* (Mestayer), Recent, New Zealand
Typhina (*Typhina*) *tetragoniatius* (Cossmann), Pliocene, India
Typhina (*Typhina*) *yatesi* (C. & F.), Recent, South Australia
Typhina (*Typhinellus*) *quadratus* (Hinds), Recent, Ecuador
Typhina (*Typhinellus*) *sowerbyi* (Broderip), Recent, Mediterranean
Typhina (*Typhinellus*) *tetrapterus* (Bronn), Pliocene, Italy
Typhina (*Typhinellus*)? *protetrapterus* (Sacco), Oligocene, Italy

Genus TYPHISOPSIS Jousseaume 1880

Type species, by original designation, *Typhis coronatus* Broderip 1833 = *T. grandis* A. Ad. 1855, Recent, Gulf of California.

Subgenus TYPHISOPSIS s.s.

Subgenus TALITYPHIS Jousseaume 1882

Type species, by original designation, *Typhis expansus* Sowerby 1874, Recent, probably Caribbean (Keen 1944, p. 56).

The varices are close behind the aperture or apertural scars and continue across the shoulder without break or decrease in size.

In *Typhisopsis* each tube is supported by a 'laminar remnant of former outer lip' (Keen 1944, p. 57), while in *Talityphis* the tubes are free. In view of the variability in the development of the outer lip (secondary varix) in *Typhinellus*, the validity of the distinction between *Typhisopsis* and *Talityphis* seems questionable.

Neither of these subgenera occurs in Australia or New Zealand.

Genus PTEROTYPHIS Jousseaume 1880

Type species, by original designation, *Typhis pinnatus* Broderip 1833, Recent, locality unknown.

Subgenus PTEROTYPHIS s.s.

Subgenus TRIPTEROTYPHIS Pilsbry and Lowe 1932

Type species, by original designation, *Typhis lowei* Pilsbry 1931, Recent, Panama.

Pterotyphis has three growth steps per whorl and very elevated flange-like varices continuous from low on the anterior canal to the previous whorl. In *Pterotyphis* s.s. the tubes are close to but not joined to the succeeding varices; in *Tripterotyphis* the tubes are coalesced with the succeeding varices. The varices are similar to those of *Typhisopsis* and for this reason *Pterotyphis* is thought to have evolved, in the late Oligocene or Miocene, from *Talityphis* by reduction of the number of growth steps in each whorl. The anomalous position of the intervariceal tubes may indicate that *Pterotyphis* is of greater antiquity, convergent with *Typhisopsis* in variceal characters.

Pterotyphis and *Tripterotyphis* are not known in Australia or New Zealand.

Genus SIPHONOCHELUS Jousseaume 1880

Type species, by original designation, *Typhis avenatus*, misprint for *T. arcuatus* Hinds 1843 (corrected by Jousseaume 1882, p. 337), Recent, South Africa.

Siphonochelus has 4.2 growth steps per whorl and rounded, fold-like varices, not

crossing the shoulder, more or less curved backward at the top and coalesced with the preceding tubes. Commonly an intervariceal axial fold is present just behind each tube.

Typical species (*arcuatus*, *fistulosus*, *solus*) have smooth, spineless varices. *Typhis parisiensis* d'Orbigny was illustrated by Cossmann (1903, pl. 2, fig. 19) as *Typhina*, and by Wrigley (1930, pl. 10, fig. 40) as *Typhis*, but was placed in *Siphonochelus* by Keen (1944, p. 66). Specimens from Barton, England (Eocene), in the New Zealand Geological Survey collection have sharp-crested varices with obsolete trough-shaped spines or crenulations on the varices. It is probably a primitive form intermediate between *Siphonochelus* and a hypothetical pre-Eocene ancestor common to *Typhis* or *Typhina*. *S. parisiensis* may require a new generic or subgeneric name.

Genus LYROTYPHIS Jousseume 1880

Type species, by original designation, *Typhis cuniculosus* Duchatel = *Murex cuniculosus* Nyst 1836, Oligocene, Belgium.

Varices as in *Siphonochelus*; five growth steps per whorl; aperture acutely angled at the bottom, encroaching on to the anterior canal. Cossmann (1903, pl. 3, figs. 4, 5) and Keen (1944, p. 54, fig. 5) show a straight anterior canal, though Cossmann stated that it is slightly bent.

Keen regarded *Lyrotyphis* as a subgenus of *Siphonochelus* and recognized only two species, *cuniculosus* and *schlotheimi*, both from the Oligocene of Europe. To these must be added *T. syringianus* Hedley, Recent, New South Wales.

Hedley (1903, p. 381) states *syringianus* has four post-nuclear whorls with twenty 'double-varices', implying five varices per whorl. A specimen from Tasmania, in the New Zealand Geological Survey collection, agrees well with Hedley's figure and description. As well as five growth steps per whorl, it has a less constricted aperture than is usual in Typhinae, with an acutely angled lower border encroaching on the anterior canal, as in the type species. The apertural rim is lower than in the other Typhinae examined, and becomes indistinct about the basal angle. Hedley's 'double-varices' consist of the varices and smaller intervariceal folds situated just behind each tube, the *costules intermédiaires* of Cossmann (1903, p. 62).

Lyrotyphis is very similar to *Siphonochelus* in all except the number of growth steps per whorl and the atypical aperture. Cossmann (1903, pp. 62–63) noted in *cuniculosus* a weak posterior channel, no more than a slight angle in the apertural border, and the extension of the aperture downward on to the anterior canal. He considered these features important, and gave full generic status to *Lyrotyphis*.

Genus SEMITYPHIS Martin 1931

Type species, by monotypy, *Semityphis incisus* Martin 1931, Upper Eocene, Java.

Semityphis has three growth steps per whorl. The smooth varices suggest closer relationship to *Siphonochelus* than to other genera.

CHECK LIST OF AUSTRALASIAN SPECIES OF TYPHINAE

Genus *Typhis*

Subgenus (*Typhis*)

maccoyi T-Woods. Oligocene (Janjukian), Australia

adventus sp. nov. Mid. Oligocene (Duntroonian–Waitakian), New Zealand

hebetatus Hutton. Upper Oligocene (Otaian), New Zealand
acanthopterus Tate. Lower Miocene (Balcomian), Australia
planus sp. nov. Lower Miocene (Altonian), New Zealand
clifdenensis sp. nov. Lower Miocene (Altonian), New Zealand
n.sp. (unnamed) Mid. Miocene (Waiauian), New Zealand
philippensis Watson. Recent, Australia
interpres Iredale. Recent, Australia

Subgenus *Hirtotyphis*

aculeatus sp. nov. Lower Miocene (Altonian), New Zealand
aoteanus sp. nov. Upper Miocene (Tongaporutuan), New Zealand

Subgenus *Neotyphis*

tepingai Fleming. Pliocene (Opoitian–Waitotaran), New Zealand

Genus *Typhina*

Subgenus *Typhina*

disjuncta (Tate). Lower Miocene (Balcomian), Australia
laciniata (Tate). Lower Miocene (Balcomian), Australia
bivariata (Verco). Recent, South Australia
yatesi (C. & F.). Recent, South Australia
pauperis (Mestayer). Recent, New Zealand

Genus *Siphonochelus*

evaricosus (Tate). Lower Miocene (Balcomian), Australia
rugicostatus Chapm. and Cressin. Pliocene (Kaiman), Australia
generosus Iredale. Recent, New South Wales
pavlova = *pavlova* Iredale. Recent, New South Wales
solus sp. nov. Recent, New Zealand

Genus *Lyrotyphis*

syringianus (Hedley). Recent, New South Wales, Tasmania

Genus *Semityphis*

? *Semityphis* sp. = *Typhis tripterus* Tate, 1888 (homonym of *T. Tripterus* Grateloup 1833). ? Pliocene, Adelaide bore, Australia

DESCRIPTION OF SPECIES

All New Zealand species are illustrated and described below, together with four Australian species from the New Zealand Geological Survey collection.

Measurements. For most species three dimensions are given in the following order: (a) height; (b) maximum diameter, i.e. including the varices, and spines if present, measured when possible between the terminal and antepenultimate varices; (c) the diameter excluding the varices and spines, measured immediately behind the terminal and antepenultimate varices. All dimensions are in millimetres. Estimated dimensions of broken specimens are given in brackets.

Genus TYPHIS Montfort

Subgenus TYPHIS

Typhis (*Typhis*) *adventus* sp. nov.

Plate 47, fig. 23; text-figs. 4, 8

Shell of moderate size, delicate, elongate, with elevated spire; peripheral angle high, shoulder narrow, base convex; varices narrow, raised folds, each with two spines visible on spire whorls, six on body whorl, the uppermost of which are of moderate size with strong backward curvature, decreasing downwards, the lowest two very small, situated on the anterior canal; tubes situated on the shoulder, higher than the tops of the varices,

inclined obliquely backwards and slightly upwards; surface of shell smooth except for growth-lines and scars of former apertures.

Dimensions. Holotype: 21 (24); 14; 11. Paratype: 21; 12.5; 10.

Repository. Holotype and paratype, New Zealand Geological Survey.

Localities. Holotype: G.S. 1473—Otiake Trig. Z, North Otago, Waitakian (Mid. Oligocene). Paratype: G.S. 1281—Wharekuri Greensand, Waitaki Valley, North Otago, Duntroonian (upper Lower Oligocene).

Age: Duntroonian to Waitakian (upper Lower to Middle Oligocene).

Remarks. *Typhis maccoyi* Tenison-Woods is close but has more acutely angled whorls, less convex base and shorter spire with suture higher on whorls, so that usually only one spine on each spire varix remains uncovered.

Typhis (Typhis) hebetatus Hutton

Plate 46, figs. 10–13; text-fig. 4 (6)

1877 *Typhis hebetatus* Hutton, p. 594, pl. 16, fig. 1.

1915 *Typhis maccoyi* Tenison-Woods; Suter, p. 28 (not *Typhis M'Coyi* Tenison-Woods 1876).

1924 *Typhis maccoyi* Tenison-Woods; Marwick, p. 328.

1926 *Typhis maccoyi* Tenison-Woods; Finlay, p. 427.

1944 *Typhis (Typhiuellus) hebetatus* Hutton; Keen, pp. 56, 65.

Shell broad, biconic, solid, of moderate size, with short spire; whorls sharply angled with a carina connecting each tube to succeeding varix; varices narrowly rounded raised folds with relatively small spines, six on each body varix, one only visible on each spire varix; sutures high on spire whorls; body whorl strongly convex; surface ornamented with faint, irregular spiral ribs in line with the variceal spines, strongest on the backs of the varices.

Dimensions. Holotype: 28.9; 20.6; 14.9. Topotype (small but with protoconch): 20.1; 13.3; 9.6. Hypotype from Bluecliffs (Pl. 46, fig. 10): 25.4; 19.8; 14.3. Hypotype from Ardgowan (Pl. 46, fig. 11): 23.3; 17.5; 13.1. Hypotype from Awamoa (Pl. 46, fig. 13): 22.6; 16; 12.3. Extra large specimen from Ardgowan: 31.5; 24.7; 17.8.

Repositories. Holotype, Otago Museum; Hypotypes, New Zealand Geological Survey.

Localities. Holotype and two topotypes, Mount Harris, South Canterbury; Ardgowan, Awamoa, Target Gully, Devil's Bridge, all near Oamaru, North Otago; Suter Coll. 159 Bluecliffs, Otaio River, South Canterbury; G.S. 162, Pareora River, South Canterbury; Otaian (upper Oligocene).

Age. Otaian–Awamoan (Upper Oligocene); Holotype: Awamoan (uppermost Oligocene).

Remarks. Specimens from the Otaian localities, Bluecliffs and Pareora River, though somewhat older than the holotype, agree closely in the development of the spines and the elevation of the spire. Specimens from the Oamaru localities Ardgowan, Awamoa, Target Gully, and Devil's Bridge have the spire consistently more depressed, with sutures reaching almost up to the peripheral angle, and generally smaller spines. The Oamaru specimens are about the same age as the type and the differences are probably attributable to varying ecological conditions.

Typhis (Typhis) planus sp. nov.

Plate 46, fig. 7

Shell small, elongate, biconic, consisting of typical protoconch and five post-nuclear whorls; peripheral angle sharp; varices narrowly rounded with only slight backward

inclination, each with six spines, the uppermost long and narrow, curving backwards and upwards, the next below prominent, lower ones tiny, diminishing progressively downwards; body whorl contracted regularly from immediately below the peripheral angle, with flattened intervariceal spaces; tubes set low, just above the peripheral angle, inclined obliquely backwards, only very slightly upwards (3° – 4° from horizontal) on adult whorls, more strongly upwards (30° from horizontal) on early whorls.

Dimensions. Holotype: 15; 10; 6.5. Paratype (protoconch missing): 19; 12; 8.

Repository. Holotype and paratype, New Zealand Geological Survey.

Localities. Holotype: G.S. 2945, Bed 6a (upper part), Clifden, Southland. Paratype: G.S. 2948, Bed 4, Clifden; Lower Altonian.

Age. Lower Altonian (Lower Miocene).

Remarks. Distinguished by small elongate form, slight backward inclination of varices, nearly horizontal tubes set low on shoulder, sharp peripheral angle and flattened variceal interspaces on the base.

Typhis (Typhis) clifdenensis sp. nov.

Plate 47, fig. 26

Shell small, elongate, biconic, with elevated spire; periphery broadly rounded; body whorl strongly convex and ventricose; varices narrowly rounded, with six spines, the lower five rudimentary, the highest one somewhat larger with only slight curvature, directed slightly upwards; tubes slightly closer to succeeding than to preceding varices, set high on the shoulder, inclined obliquely backwards and relatively steeply upwards (35° to 40° from horizontal on adult whorls, about 45° on the earliest whorl).

Dimensions. 16 (C. 18); 10.5; 7.

Repository. New Zealand Geological Survey.

Age and locality. Holotype (the only specimen), G.S. 2937, 'Long Beach', Clifden, Southland, upper Altonian (Lower Miocene).

Remarks. The tubes are more steeply inclined than in any other species of *Typhis* s.s. A related, but probably distinct, form with less steep tubes, from the Awamoan of Rifle Butts, Oamaru, is represented by a single specimen in the collection of the Geology Department, Victoria University, Wellington.

EXPLANATION OF PLATE 46

Figure 7 $\times 3$; all other figures $\times 2$.

Figs. 1, 3. *Typhis (Hirtotyphis) aculeatus* sp. nov., 1, Holotype, 3, Paratype G.S. 2155.

Fig. 2. *Typhis (Hirtotyphis) aoteanus* sp. nov., holotype.

Fig. 4. *Typhis (Typhis)* sp. nov. G.S. 3839, Dovedale.

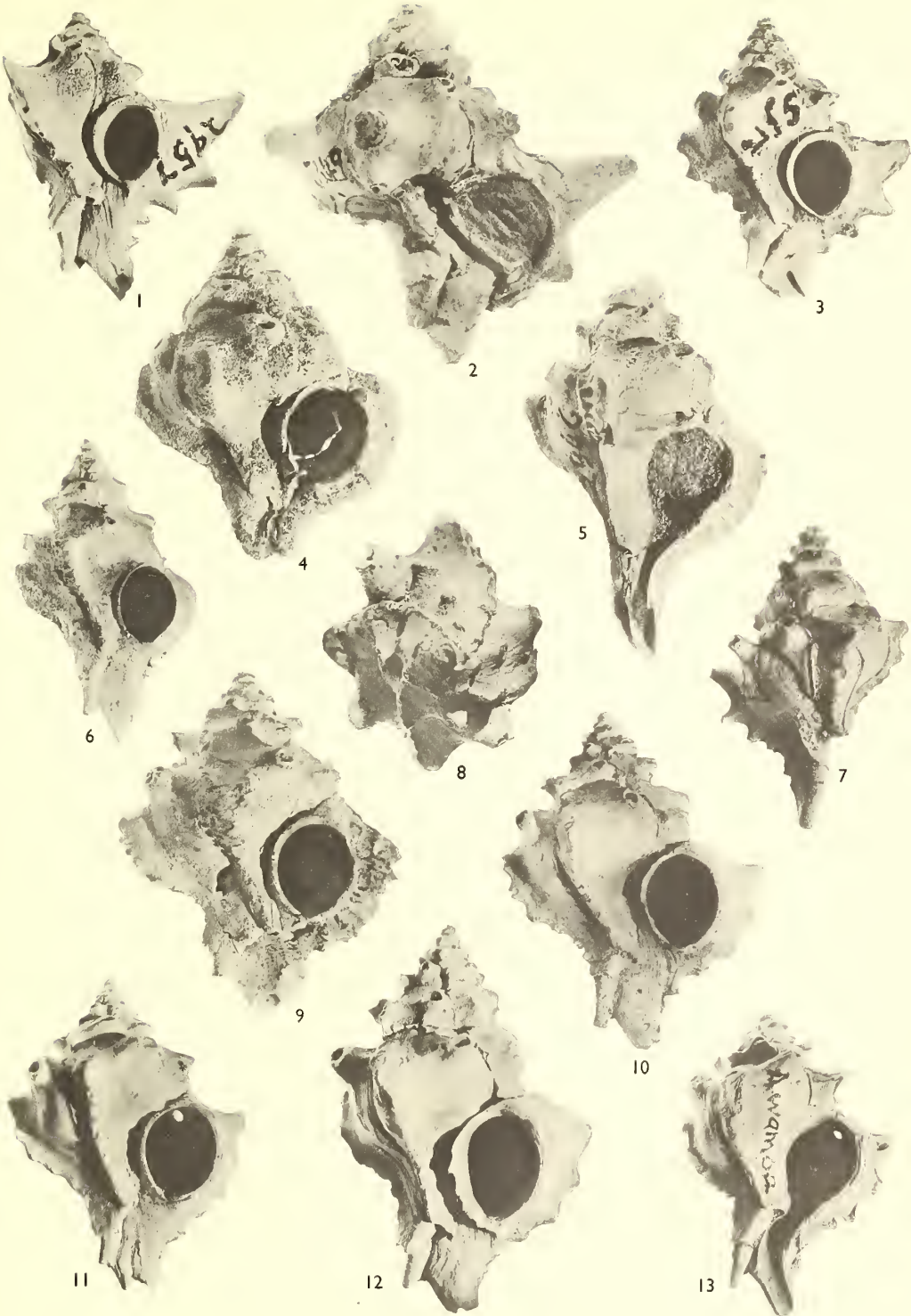
Fig. 5. *Rugotyphis francescae* (Finlay) gen. nov., topotype.

Fig. 6. *Rugotyphis* cf. *francescae* (Finlay) gen. nov. G.S. 2937, 'Long Beach', Clifden.

Fig. 7. *Typhis (Typhis) planus* sp. nov., holotype.

Figs. 8, 9. *Rugotyphis secundus* gen. et sp. nov. 8, Apical view of paratype, V. 79, Clifden (bed 7?), Southland. 9, Holotype.

Figs. 10–13. *Typhis (Typhis) hebetatus* Hutton. 10, Suter Coll. 159, Bluecliffs, S. Canterbury. 11, Ardgowan, Oamaru. 12, Holotype. 13, Showing incomplete terminal varix, Awamoan, Oamaru.



VELLA, Australasian Typhinac

Typhis (Typhis) sp. nov.

Plate 46, fig. 4

This species is represented by a single, apparently badly worn specimen. Of moderate size, broadly biconic, with short, but acuminate spire; tubes set only slightly above the tops of the varices, inclined obliquely backward and slightly above horizontal; varices seem rather broad and rounded, convex in front, deeply excavated behind, and have borne six or seven spines which are worn quite away; differs from all other species in the profile of the body whorl and its varices which descend vertically from the poorly defined peripheral angle, then turn very rapidly under to join the anterior canal.

Dimensions. 24.5; 19; 14.

Repository. New Zealand Geological Survey.

Locality. G.S. 3839, Dovedale, North Canterbury.

Age. Waiauan (upper Middle Miocene).

Typhis (Typhis) maccoyi Tenison-Woods

Plate 47, fig. 25; text-fig. 4 (10)

1876 *Typhis M'Coyi* Tenison-Woods, p. 22, pl. 1, fig. 5.

1888 *Typhis M'Coyi* Tenison-Woods; Tate, p. 92.

1903 *Typhis (Typhina) maccoyi* Tenison-Woods; Cossmann, p. 58, pl. 2, fig. 16.

1944 *Typhis (Typhinelus) maccoyi* Tenison-Woods; Keen, pp. 56, 66.

The following description is based on eight specimens from Spring Creek, Torquay, Victoria.

Shell of moderate size, moderately elongate, biconic, with elevated spire; peripheral carina prominent; base gently convex, contracting sharply from the periphery; usually only one spine showing on spire varices, sometimes the second not covered by the following whorl; body varices with six moderately large backward-curving spines; tubes inclined obliquely backward and only slightly upward.

Dimensions. Hypotype: 22.0; 14.4; 11.2.

Localities. Holotype from Table Cape, Tasmania; specimens in New Zealand Geological Survey collection from Spring Creek, Torquay, Victoria.

Age. Janjukian (Oligocene).

Remarks. The Spring Creek specimens seem stouter than Tenison-Woods's illustration.

Several authors have regarded *T. hebetatus* as a synonym of *T. maccoyi*, but *T. hebetatus* is much stouter, with a shorter spire, smaller spines, and a more convex base. *T. adventus* sp. nov., closer to *maccoyi*, is easily distinguished by its still more elevated spire and more convex body whorl.

Subgenus *HIRTOTYPHIS* Jousseaume
Typhis (Hirtotypis) aculeatus sp. nov.

Plate 46, figs. 1, 3

Shell of moderate size, solid, broadly biconic with somewhat depressed spire; shoulder broad and sloping, peripheral angle distinct, but not sharp, almost reached

by sutures on spire whorls; base strongly convex; varices prominent, rounded folds with slight backward inclination, each surmounted by five spines with very slight backward curvature, diminishing downwards, the second lowest situated at the point of maximum concavity between the body and the anterior canal, lowest on the upper part of the canal; below it, and slightly behind the crest of the varix, an oblique ridge, which in some paratypes is produced to form an obsolete spine offset slightly backwards from the higher spines; upper three spines grotesquely large; tubes set low on the shoulder, bent obliquely backwards and upwards at 10° from horizontal; three or four faint spiral ribs on the base of some specimens, some in line with variceal spines, others not.

Dimensions. Holotype: 24; not determinable; 11.5. Paratype (Pl. 46, fig. 3): 21; 17; 10. Topotype-paratype: 18; 14; 9.

Repository. Holotype and four paratypes, New Zealand Geological Survey.

Localities. Holotype and three paratypes, G.S. 2957, North Bank, Waiau River, Clifden, Southland; one paratype, G.S. 2155, North Bank, Clifden; Altonian. A doubtful worn specimen, G.S. 2946, Bed 6a, Clifden, Lower Altonian.

Age. Altonian–Clifdenian? (Lower Miocene). Holotype: Altonian?

Remarks. This species is undoubtedly intermediate between the later *Hirtotyphis* with three spines on each varix (*horridus*, *aoteanus*) and the more conservative typical *Typhis* with spines of moderate to small size. *T. planus* sp. nov. may be related, but has much smaller spines and is retained in *Typhis* s.s.

Although morphologically close to *Typhis* s.s., *T. aculeatus* is more appropriately classed as *Hirtotyphis*.

Typhis (Hirtotyphis) aoteanus sp. nov.

Plate 46, fig. 2

Shell large for the genus, broadly biconic, squat, solid, spire depressed; periphery broadly rounded; sutures immediately below uppermost variceal spines on spire whorls; base convex, but shape distorted by crushing; varices low, broadly rounded, surmounted by three straight, radial spines, the uppermost grotesquely large, the next intermediate in size, the lowest, on the base, quite small; tubes set high on the shoulder with narrow interspace to the variceal spine on the preceding whorl, inclined obliquely backward and upward at 30° from horizontal.

Dimensions. 27 (31+); 28; 17.

Repository. Holotype, New Zealand Geological Survey.

Locality. Holotype G.S. 5349, Hurupi Formation, Pahaoa River, East Wairarapa. A juvenile from a nearby locality in the Hurupi Formation.

Age. Lower Tongaporutuan (base of Upper Miocene).

Remarks. An illustration by Cossmann (1903, pl. 2, fig. 24) of *Hirtotyphis horridus* (Brocchi), from the Pliocene of Italy, shows a smaller shell with similar low rounded varices. Cossmann notes the straightness of the spines. The shell from the Miocene of Hungary (Hoernes 1856, pl. 26, fig. 9) has the spines curved slightly backward.

The remarkable similarity of the European and New Zealand species is attributed to close genetic affinity and not to convergent evolution.

Subgenus NEOTYPHIS nov.

Typhis (Neotyphis) tepungai Fleming

Plate 47, figs. 27, 28; text-fig. 4 (9)

1943 *Typhis tepunga* Fleming, p. 205, pl. 30, fig. 21.

Shell of moderate size, elongate, fusiform, with elevated spire; peripheral angle at the middle of spire whorls, becoming ill-defined on the adult whorls; base convex; varices broadly rounded, moderate folds, convex in front, a little excavated behind.

For other details see description of the subgenus, above.

Dimensions. Holotype (lacking protoconch): 21·5; 13; 10·5. Paratype (G.S. 2499): 21; 11; 9.

Repository. Holotype and three paratypes, New Zealand Geological Survey.

Localities. Holotype and paratype with intact protoconch, G.S. 2661, Tahoraite Survey District, Southern Hawkes Bay; paratype, G.S. 2499, Tahoraite Survey District; paratype, G.S. 2314, Takapau Survey District, Southern Hawkes Bay; Waitotaran (Upper Pliocene). Figured specimen (Pl. 47, fig. 28), G.S. 1561, Waiau River, 10 chains below Mangaone junction, Wairoa Survey District, Northern Hawkes Bay, Opoitian (Lower Pliocene). Cliffs east of Whangaimoana, Palliser Bay, Southern Wairarapa, Kapitean or basal Opoitian (uppermost Miocene or basal Pliocene).

Age. Kapitean to Waitotaran (uppermost Miocene to Upper Pliocene).

Remarks. The trivial name *tepunga* is formed from a patronymic, and, at the request of Dr. C. A. Fleming, is changed to *tepingai* to conform with the International Rules.

The varices of *Neotyphis tepungai* differ from those of all other New Zealand species. *Typhis (Typhis) clifdenensis* sp. nov., with its elongate form, reduced variceal spines and steeply inclined adult tubes is probably close to the ancestor of *Neotyphis*.

Genus RUGOTYPHIS nov.

Rugotyphis francescae (Finlay)

Plate 46, fig. 5

1924 *Typhis francescae* Finlay, p. 465, pl. 49, figs. 6a, 6b.1944 *Typhis (Typhinellus) francescae* Finlay; Keen, pp. 56, 65.

Shell large for the subfamily, solid, with rhomboidal outline; periphery sharply angled below the middle of spire whorls; shoulder broad, sloping, flattened; front of each body varix with one rib at the peripheral angle larger than the remainder, between this and the base of the aperture six or seven parallel, irregular ribs sloping gently downward from the apertural rim; no ribs on the varix below the level of the base of the aperture; on the section of varix crossing the shoulder three or four weak parallel ribs sloping steeply upwards from the apertural rim; five or six tiny trough-shaped spines on the crest of each varix not all in line with the variceal ribs, the uppermost at the peripheral angle, a little larger than the remainder; tubes situated just above the peripheral angle, inclined very slightly backwards and upwards; surface between varices smooth except for growth-lines.

Dimensions. (After Finlay) height 34 mm.; diameter 23 mm.

Repository. Holotype, Auckland Institute and Museum. Hypotype, New Zealand Geological Survey.

Localities. Holotype and hypotype, Bed 6a, Clifden, Southland; a fragment from Bed 4, Clifden;

Lower Altonian (Lower Miocene). A small and non-typical specimen (Pl. 46, fig. 6) from G.S. 2937, 'Long Beach', Clifden, Upper Altonian (Lower Miocene).

Age. Altonian (Lower Miocene).

Remarks. The hypotype, though broken, is nearly as large as, and agrees well with, the type. The fragment from Clifden bed 4 is an anterior canal with a portion of varix attached. The upper Altonian specimen illustrated is a less adult shell than the type with about five post-nuclear whorls (apex missing); it is considerably smaller than the lower Altonian specimens would be at the same stage of development, and differs further in having four lamellar spines on the varices below the lowest rib, two being situated on the canal.

Rugotyphis secundus sp. nov.

Plate 46, figs. 8, 9

Shell of moderate size, solid, broadly biconic, differing from *francescae* in having a more depressed spire with sutures higher on the whorls, almost reaching the peripheral carina, body whorl contracting more sharply from the periphery, tubes quite radial, variceal spines extending down to the anterior canal which is shorter, very broad and flattened.

Dimensions. Holotype: 25; 20.5; 15. Paratype: 24; 18; 13.

Repositories. Holotype, New Zealand Geological Survey. Paratype, Geology Department, Victoria University of Wellington.

Localities. Holotype G.S. 2155, left bank, Waiau River, Clifden, Southland, upper Altonian (Lower Miocene). Paratype V. 79, ? bed 7, Clifden, Lilburnian (Middle Miocene).

Age. Upper Altonian? to Lilburnian? (Lower to Middle Miocene?).

Genus TYPHINA Jousseaume

Subgenus TYPHINA s.s.

Typhina (*Typhina*) *pauperis* (Mestayer)

Plate 47, fig. 24; text-fig. 4 (7)

1916 *Typhis pauperis* M. K. Mestayer, p. 127, pl. 12, figs. 9, 9a.

1944 *Typhis* (*Typhinellus*) *pauperis* Mestayer; Keen, pp. 56, 66.

Shell very small, moderately elongate, pagodiform, thin and fragile, three and three-quarter post-nuclear whorls with carinate periphery high on spire whorls; base tapering from the periphery, lightly convex; no secondary varices; primary varices not extending on to the anterior canal, crenulated by three deep radial folds, each bearing a prominent trough-shaped spine curving gently inwards towards the spire and backwards; tubes straight, pointing slightly backward and upward; anterior canal narrow, slightly flattened, bent gently to right.

Dimensions. Holotype: 8; 5; 3.2.

Repository. Holotype (M. 1749) and paratype (M. 779) Dominion Museum, Wellington.

Localities. Holotype 58–60 fathoms off Poor Knights Island, paratype 25–30 fathoms off Hen and Chickens Islands, Hauraki Gulf. One specimen (M. 11067) 113–120 fathoms, off Mayor Island, Bay of Plenty (same locality as *Siphonochelus solus*).

Age. Recent.

Remarks. *Typhina pauperis* is distinguished from other species mainly by its small size, regularly tapering body whorl, and lack of secondary varices.

Typhina (Typhina) yatesi (Crosse & Fischer)

Plate 47, fig. 16; text-fig. 4 (5)

- 1865 *Typhis yatesi* Crosse & Fischer, p. 54, pl. 2, fig. 3.
1866 *Typhis yatesi* C. & F.; Sowerby, p. 319, pl. 284, figs. 20, 21.
1874 *Typhis yatesi* Angas; Sowerby, pl. 3, fig. 14.
1880 *Typhis yatesi* Angas; Sowerby, pl. 284 *bis*, figs. 22, 23.
1880 *Typhis yatesi* C. & F.; Tryon, pl. 30, fig. 294.
1939 *Typhis yatesi* C. & F.; Smith, p. 19, pl. 14, fig. 8.
1944 *Typhis (Typhinellus) yatesi* C. & F.; Keen, pp. 56, 68.

Shell of moderate size, rather broad, with moderately elevated spire; peripheral angle poorly defined, high on whorls; base strongly convex, subquadrate in profile; no secondary varices; primary varices stopped above the anterior canals, but represented on each anterior canal of the body whorl by a large, flat, triangular, fin-like spine; adult variceal spines partly trough-shaped, partly tubular, the sides having curled around far enough to meet and become soldered together for about half the length of each spine.

Dimensions. Hypotype: 16.5; 9.6; 7.6.

Repository. Hypotype, New Zealand Geological Survey.

Localities. Holotype, Gulf of Saint Vincent, South Australia; hypotype, South Australia (no other details available).

Age. Recent.

Remarks. Though smaller than many Typhinae *T. yatesi* is extraordinarily large for *Typhina*. It is distinguished by its size, convex body, partly tubular variceal spines, and fin-like development of the varices on the anterior canal.

Typhina (Typhina) bivaricata (Verco)

Plate 47, fig. 20; text-figs. 4 (1), 4 (2)

- 1909 *Typhis bivaricata* Verco, p. 272, pl. 21, figs. 1–2.
1944 *Typhis (Typhina) bivaricatus* Verco; Keen, pp. 55, 63.

Shell very small, biconic, compact, with moderately elevated spire; peripheral angle high on whorls; base moderately convex; secondary varices nearly as large as the primary varices, extending from top to bottom of the outer edge of the aperture; primary varices decreasing downwards, not reaching the anterior canals.

Dimensions. Hypotype height 4.8, maximum diameter 3.0 mm.

Repository. Hypotype (cotype), New Zealand Geological Survey.

Locality. 104 fathoms, 35 miles south-west of Neptune Islands, South Australia.

Age. Recent.

Remarks. *T. bivaricata* is distinguished from all other species by the extraordinary development of its secondary varices.

Genus SIPHONOCHELUS Jousseaume
Siphonochelus solus sp. nov.

Plate 47, fig. 21

Shell small, elongate, fusiform, solid, apex worn, final two growth steps mostly broken off, four and a half whorls intact; peripheral angle high, shoulder narrow and deeply channelled behind tubes and varices; spire whorls contracting slightly below periphery; base gently convex, contracting gradually to the anterior canal; varices rounded oblique folds raised above the shoulder and curved back to join the preceding tubes; in front of each varix a deep sulcus about one-third of a growth stage in width, containing apertural scars slightly in front of the middle; sulcus followed by a broad rounded fold initiating the next growth step, decreasing downwards and dying before reaching the anterior canal; tubes all worn down to stumps, directed steeply upwards and obliquely backwards, flattened, broadened in the spiral direction extending from the initial fold to somewhat behind the varix to which it is united; below the tube, between the initial fold and the varix, a broad shallow concavity about two-thirds the width of the total growth step; surface of shell smooth except for growth-lines; aperture not seen.

Dimensions. Height 8 mm.; maximum diameter 4 mm.

Repository. Holotype (the only specimen) (M. 11067), Dominion Museum, Wellington.

Locality. 113–130 fathoms off Mayor Island, Bay of Plenty.

Age. Recent.

Remarks. *Siphonochelus solus* seems close to the South African species *S. arcuatus* judged by the figures of Tryon (1880, pl. 30, fig. 293) and Keen (1944, p. 54, fig. 11). *S. solus* is distinguished by its broad, flattened intervariceal tubes.

The holotype of *S. solus* and a specimen of *Typhina pauperis* were dredged from the same locality. Both are chalky, broken shells, and these species may not be living there now.

EXPLANATION OF PLATE 47

Figs. 14, 15, 19. *Typhina* (*Typhinellus*) *sowerbyi* (Broderip), photographs of illustrations of Reeve (1842, pl. 240, figs. 7–9), magnification not known.

Fig. 16. *Typhina* (*Typhina*) *yatesi* (Crosse and Fischer), Recent, South Australia, $\times 3$.

Figs. 17, 18. *Typhina* (*Typhina*) *belcheri* (Broderip), photographs of illustrations of Reeve (1842, pl. 240, figs. 5, 6), magnification not known.

Fig. 20. *Typhina* (*Typhina*) *bivaricata* (Verco) co-type, 104 fathoms, off Neptune Islands, South Australia, $\times 7$.

Fig. 21. *Siphonochelus solus* sp. nov., holotype, $\times 4$.

Fig. 22. *Lyrotyphis syringianus* (Hedley), Port Esperance, Tasmania, $\times 6$.

Fig. 23. *Typhis* (*Typhis*) *adventus* sp. nov., holotype, $\times 3$.

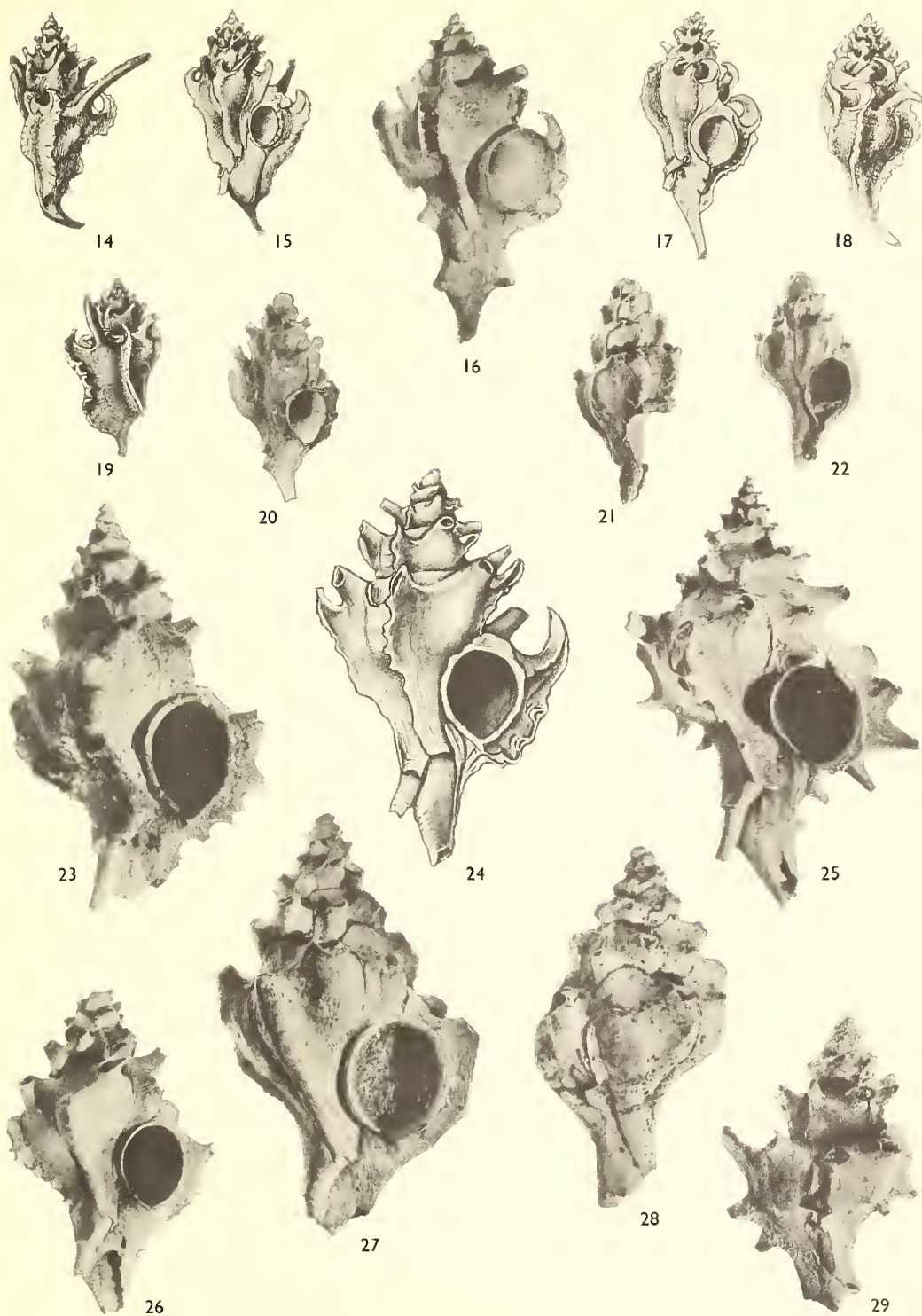
Fig. 24. *Typhina* (*Typhina*) *pauperis* (Mestayer), holotype, $\times 7$.

Fig. 25. *Typhis* (*Typhis*) *maccoyi* Tenison-Woods, Spring Creek, Victoria, $\times 3$.

Fig. 26. *Typhis* (*Typhis*) *clifdenensis* sp. nov. holotype, $\times 3$.

Figs. 27, 28. *Typhis* (*Neotyphis*) *tepungai* Fleming subgen. nov.; 27, holotype $\times 3$; 28, G.S. 1561 Wairoa, Northern Hawkes Bay, $\times 3$.

Fig. 29. *Typhis* (*Typhis*) *pungens* (Solander), Barton, England, $\times 3$.



Genus *LYROTYPHIS* Jousseaume*Lyrotyphis syringianus* (Hedley)

Plate 47, fig. 22; text-figs. 4 (3), 4 (4)

1903 *Typhis syringianus* Hedley, p. 381, text-fig. 94.1944 *Siphonochelus* (*Siphonochelus*) *syringianus* (Hedley); Keen, pp. 58, 67.

Shell tiny, broadly biconic, solid; whorls rounded, without perceptible peripheral angle; base moderately convex; tubes ovate, slightly elongated in the spiral direction, inclined steeply upward, very slightly backwards; varices curved back at the top to join the tubes; broad rounded intervariceal folds just behind tubes; apertural scars in the sulcus behind the intervariceal folds; surface smooth except for growth-lines; for other details see generic description.

Dimensions. Hypotype: height 4.4 mm., maximum diameter 2.5 mm.

Repository. Hypotype, New Zealand Geological Survey.

Localities. Holotype, 41–50 fathoms, Cape Three Points, New South Wales, Australia; hypotype, Port Esperance, Tasmania.

Age. Recent.

Acknowledgements. Specimens of Recent New Zealand shells were lent by the Dominion Museum, Wellington, the holotype of *Typhis hebetatus* Hutton by the Otago Museum, and most of the fossil specimens by the New Zealand Geological Survey. Also available from the Geological Survey, and of particular value, were several overseas specimens. The University of New Zealand Research Grants Committee gave financial assistance.

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REEF-CONTROLLED DISTRIBUTION OF DEVONIAN MICROPLANKTON IN ALBERTA

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ABSTRACT. Upper Devonian hystrichospherids of the off-reef Duvernay facies in Alberta, Canada, can be combined into three artificial groups that have different distribution patterns with regard to reefs. Simple spherical forms are widespread, from beds inter-fingering with reef carbonate into off-reef areas. Thin-spined species are also widespread, but are seldom found within one mile of reefs. Thick-spined and polyhedral forms occur in off-reef strata, but seldom near reefs. All types increase in abundance with increasing distance from reefs. Plant spore distribution is useful in determining major current patterns. Forty species of hystrichospherids are described. New genera proposed are *Duvernaysphaera*, *Multiplisphaeridium*, and *Paleopedicystus*. *Micrhystridium* and *Leiosphaeridium* are emended. New morphological structures of Chitinozoa are described and *Hoegisphaera* is proposed as a name for a new type of Paleozoic microfossil possibly allied to the Chitinozoa.

THE Duvernay member is interpreted as the off-reef calcareous shale equivalent of the Leduc reef-bearing carbonates of the Woodbend formation in central Alberta. Acid-resistant microfossils, including hystrichospherids, plant spores, Chitinozoa, and scolecodonts, are present in Duvernay sediments. These fossils were studied in order to determine if reef trends had influenced their distribution in the near-reef equivalents. Approximately sixty wells penetrating the Duvernay shale were used in the study. For the most part, the samples were decontaminated rotary cuttings from the microlithologically recognizable upper part of the member.

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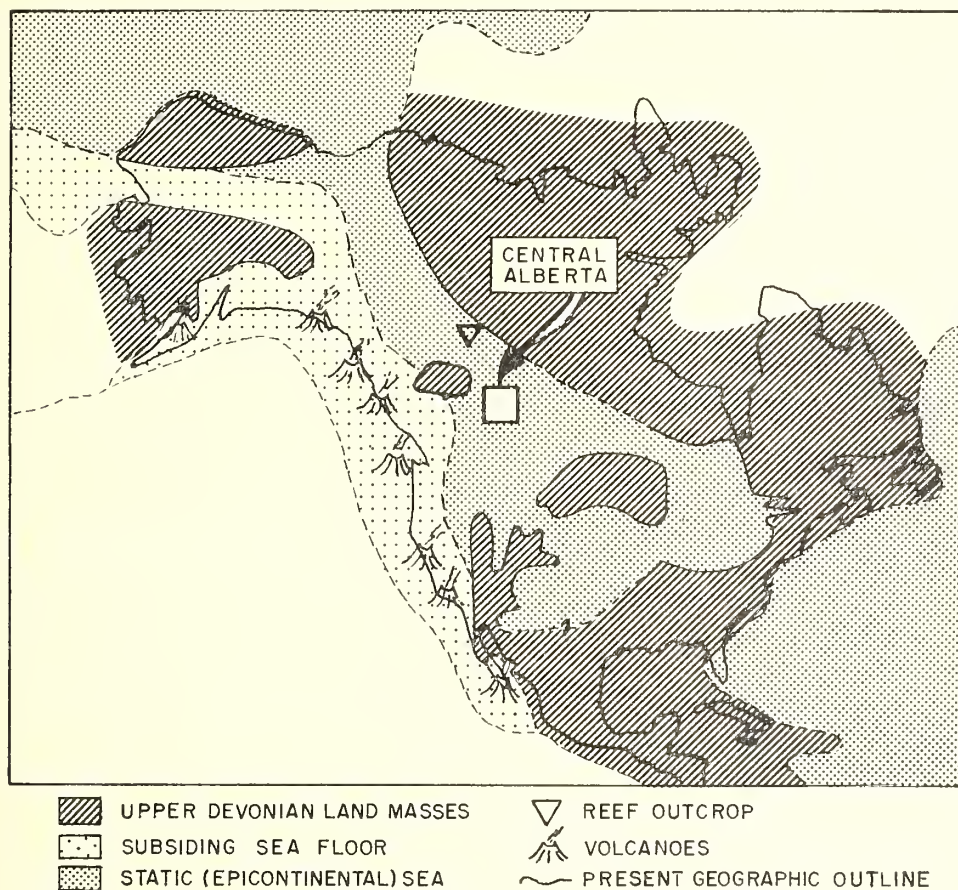
GENERAL GEOLOGY

During Upper Devonian time, much of western Canada and the United States was covered by epicontinental seas, with the exception of an interrupted volcanic belt located approximately along the present Pacific coastline (text-fig. 1). The sea at one time extended as far east as central New York, although in Middle and Lower Upper Devonian times the seas in western North America did not communicate with those to the east. On islands in the shallow seas and on the adjacent land masses grew a variety of spore-bearing plants. Reefs of biohermal form, composed of remains of algae, stromatoporoids, bryozoans, corals, and numerous other organisms, in addition to fragmental and chemically deposited carbonate, were formed in Alberta. These are now reservoirs for much of Canada's proven oil.

Woodbend formation. This group (text-fig. 2) includes a lower fragmental limestone, the Cooking Lake member; a middle portion grading laterally from the Leduc reef facies to the Duvernay dark calcareous shale; and an upper dolomite and calcareous shale, the Ireton member. These units can generally be recognized on electric logs, although their contacts are transitional. The generalized descriptions given below do not hold outside of the general Edmonton area of Alberta. Because of the essential unity and

transitional nature of these sediments, they are here considered as members, following the original interpretation of the Imperial Oil staff (1950).

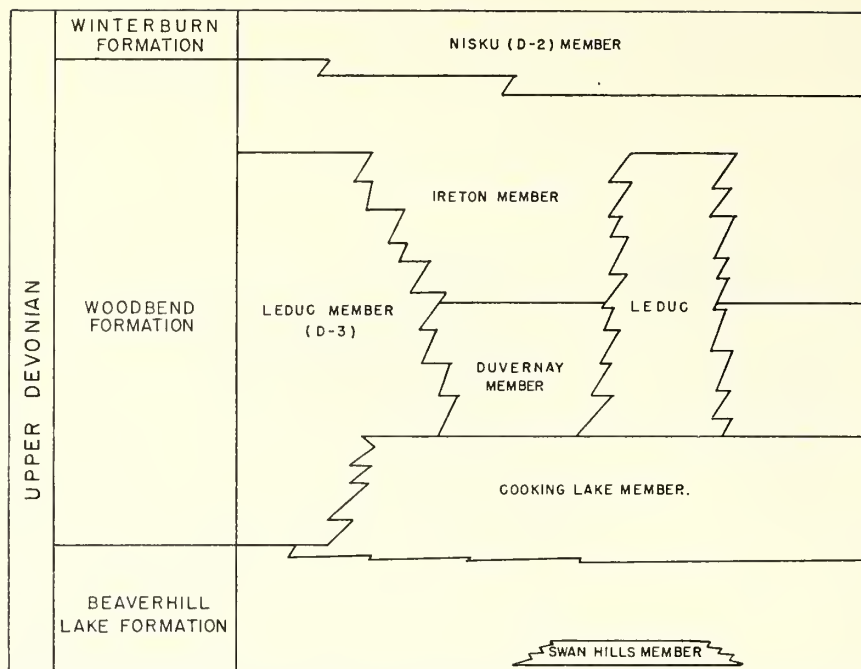
1. *Cooking Lake member*. The base of this member is placed at the change from the argillaceous limestones of the Beaverhill Lake formation to the fragmental limestones



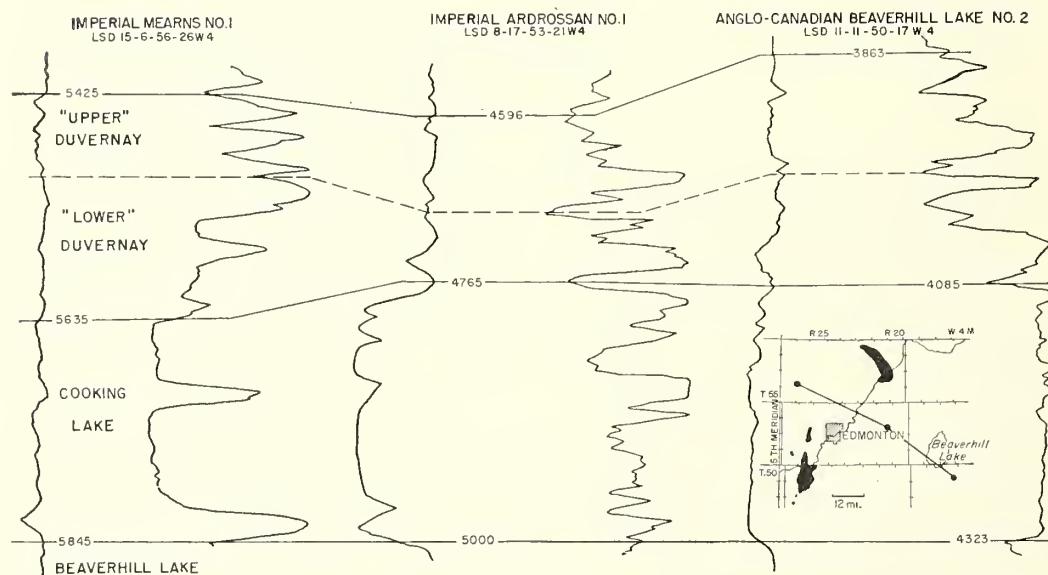
TEXT-FIG. 1. Upper Devonian paleogeograph of North America. Revised from H. and G. Termier 1952, with new limits.

above; the contact is transitional. At the upper contact, the limestones become interbedded with the shales of the Duvernay member in off-reef areas. In part, the unit is biostromal. In some areas the formation is continuous with the Leduc member, especially along the Morinville–Rimbey trend, the Bashaw trend, and in the Killam area (text-fig. 8). West of the Rimbey trend the Cooking Lake is often represented by a shale equivalent.

2. *Duvernay member*. The basal contact of the Duvernay with the Cooking Lake member is picked somewhat arbitrarily. The upper part of Cooking Lake contains black shale



TEXT-FIG. 2. Divisions of the Upper Devonian Woodbend formation, central Alberta.



TEXT-FIG. 3. Typical electric logs of the Duvernay member, Woodbend formation, Alberta.

stringers that are similar to the dark-brown to black calcareous shales and shaly limestone of the basal Duvernay. In reef areas the Duvernay is quite thin, but it may be more than 300 feet thick in off-reef areas. The upper part of the Duvernay has a characteristic curve on electric logs (text-fig. 3). Essentially, it consists of hard, dark brownish-black (5YR 2/1), impure interbedded limestone and shale having angular fracture and high organic content. Large volumes of sediment of equivalent age outside the immediate Edmonton area are grey to grey-green shales.

3. *Leduc member*. This member includes all biohermal and biostromal bodies of the carbonate complex of the Woodbend formation. Most Leduc reefs are dolomitized, but Golden Spike, Redwater, and others are limestone or are only partly dolomitized. The majority of the reefs of the Morinville–Rimbey trend seem to be equivalent, at least in part, to the off-reef Duvernay member.

4. *Ireton member*. The lower part of the Ireton, above the Duvernay, is generally a greenish calcareous shale but locally may be dark coloured and rich in organic matter. The upper part is argillaceous dolomite. Its thickness ranges from about 10 feet, above some of the Leduc biostromes, to 700 or more feet in off-reef areas, where it overlies the Duvernay member. In general, its residues are characterized by less organic material than are those from the Duvernay member.

TYPES OF MICROFOSSILS

Hystrichospherids, plant spores, scolecodonts, and Chitinozoa are the types of acid-resistant fossils on which the interpretations given in this report are based. Descriptions of the species of hystrichospherids, one new chitinozoan (?), and morphological notes on *Angochitina* are appended.

Hystrichospherids. A heterogeneous group of fossil and Recent microscopic organisms is included in the hystrichospherids. Some, particularly from Mesozoic and Tertiary sediments, are known to be stages in the life cycles of dinoflagellates and other algae. Others perhaps are encysted stages of Bryozoa and extinct flagellates and eggs of Crustacea, but many, particularly Paleozoic forms, cannot be assigned to any extant group. Some resemble chrysophytes.

These organisms vary from simple spherical bodies to complex forms having spines, enveloping lacy networks, membranes, and other ornamentation. Their size range is from 5 to over 120 microns. They are largely insoluble in most acids and can stand fairly long treatments with hydroxides. They occur in most marine clays and shales, in cherts and fine-grained limestones, and occasionally in evaporites. Hystrichospherids have been found mostly in saline waters or in sediments containing marine organisms. Some species are good for age determinations.

Plant spores. Because they represent land plants, plots of relative plant spore abundance will indicate land masses and islands that became stabilized above water-level. Upper Devonian plant spores are quite diversified and are valuable in correlations. Many of the types described from the U.S.S.R. by Naumova (1953) are present in sediments of western Canada.

Chitinozoa. These are extinct acid-resistant, tube- to flask-shaped organisms, which are

frequently ornamented with spines. The normal size of Devonian species is at least 150 microns, and they can be picked from samples in the same way as ostracodes and foraminifera. Some workers attribute Chitinozoa to various phyla, but on little real evidence. They most closely resemble cysts of chrysomonads, especially *Ochromonas*, but the resemblance is probably superficial. Their known stratigraphic range is Ordovician to Lower Pennsylvanian, but their greatest abundance is in the Devonian. Chitinozoa are useful for determining both age and environment and therefore should be sought with other microfossils.

Other organisms. Scolecodonts (jaws of marine worms), mostly belonging to the genus *Arabellites*, are occasionally present, especially in the same samples with Chitinozoa.

INTERPRETATION

Hystrichospherid species and growth-forms. Approximately fifty species are recognized in the Duvernay member. With rare exceptions the species of hystrichospherids are the same as those of the Ireton and Cooking Lake members, although they occur in different proportions. Most of the species recognized in the Upper Devonian sediments of the Edmonton area can be combined artificially into three main types, or *growth-forms* (text-fig. 4), which have different patterns of distribution with regard to reefs. These three forms are the basis for the interpretations presented in this report.

1. Simple, spherical forms. The surface is smooth, papillate, or ciliate.
2. Thin-spined forms. The spherical central body bears long, thin spines that do not seem to be an integral part of the central body.
3. Polyhedral, thick-spined and saccate forms. The processes are very broad at their bases, are often hollow and seem to be extensions of the central body of the organism.

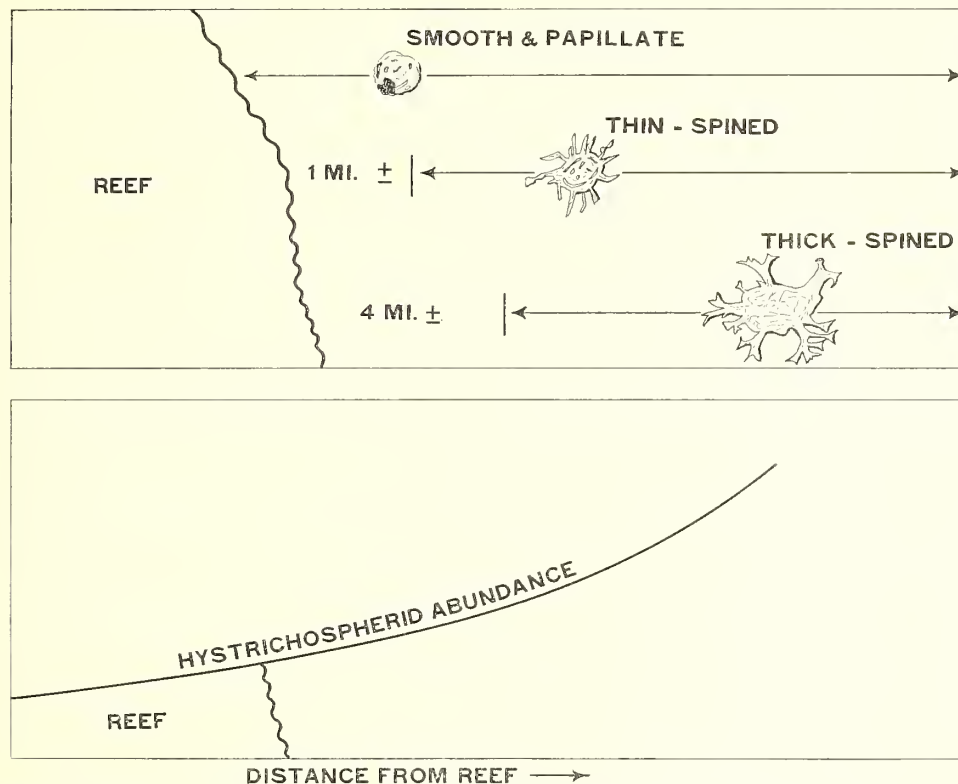
Hystrichospherid distribution. Hystrichospherids are generally much more abundant in off-reef than in near-reef strata (text-fig. 4). This could be a result of several factors:

1. Their optimum environment is the quiet, deeper water of the off-reef areas.
2. Wave action in shallow water near the reefs may have destroyed or winnowed out their remains.
3. Diagenetic processes might have destroyed the microfossils in the coarser, near-reef sediments.
4. Scavengers might have destroyed the organisms.

The environment factor is considered the most important because only one growth-form of hystrichospherid is most prevalent near the reefs, and the others are added with distance from the reefs. It is unlikely that there was selective destruction by wave action, scavengers, or diagenesis. Also, other acid-insoluble microfossils (Chitinozoa, plant spores) are not affected in this way. There are, moreover, areas of sediment moderately high in fragmental carbonate in which all types are present.

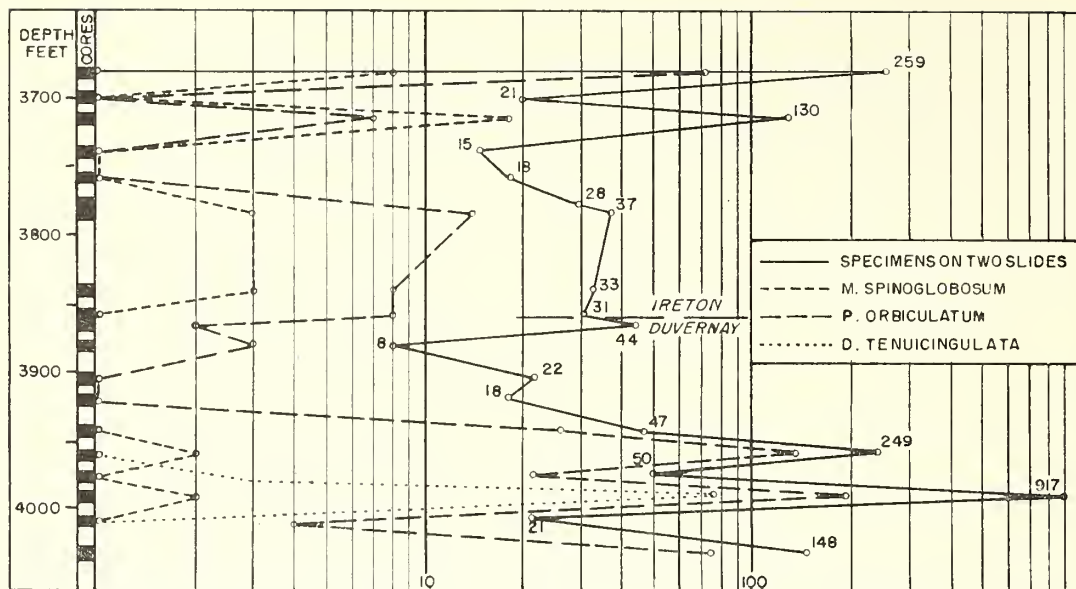
Considerable variations in the number of hystrichospherids occur at each sampled interval in cored wells. Text-figs. 5 and 6 show the total abundance of hystrichospherids in part of the Ireton-Duvernay section for the Anglo-Canadian Beaverhill Lake No. 2 well and for the A. H. C. and E. Camrose No. 1 well. In the former, the numbers increase, within less than 10 feet of vertical distance, from fifty individuals per two slides

to 917 individuals per two slides (this represents, very approximately, 1 gramme of sample). The abundance of selected hystrichospherid species for the same two wells also varies greatly (text-fig. 7). The vertical sequence is similar for both wells, and for others counted in this manner, but long-cored intervals are not available from enough wells to check the feasibility of correlating Woodbend sediments by this method.

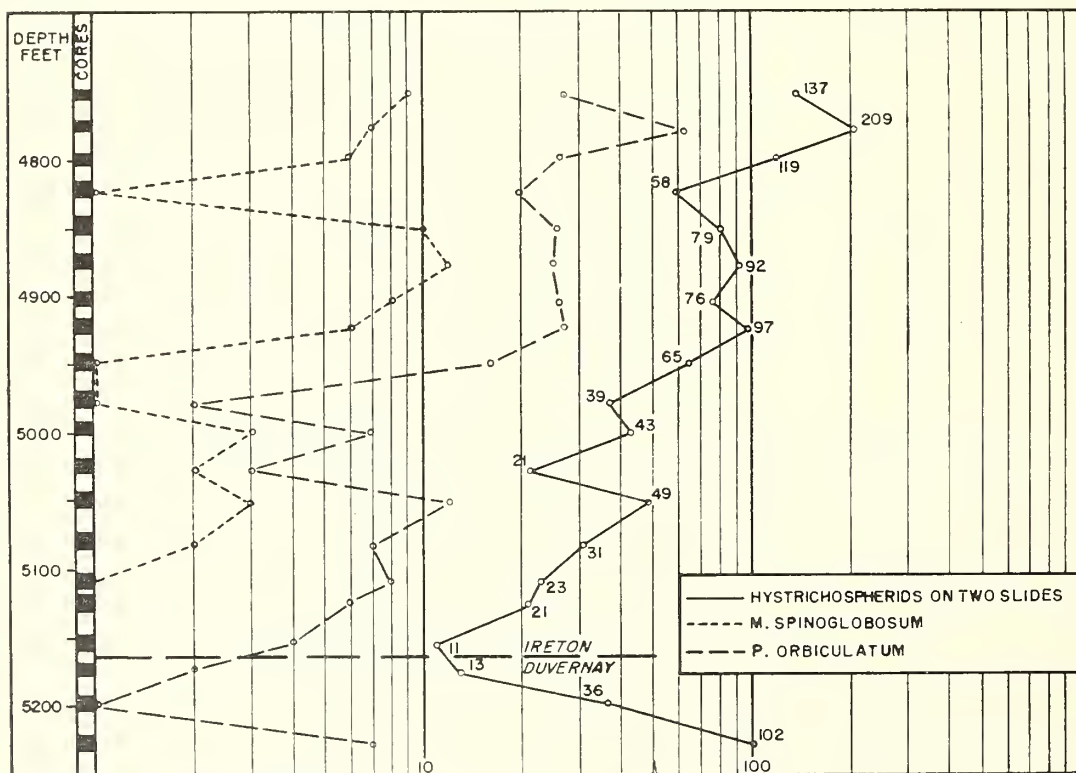


TEXT-FIG. 4. Diagrammatic representation of distribution of hystrichospherid growth forms, Upper Devonian, central Alberta.

Considering distribution by growth-form, simple spherical forms are widespread in the Duvernay strata of the Edmonton area (text-fig. 8). They occur all the way from shales interbedded with reef carbonate (Redwater Saltwater disposal well, T57, R21, W4th M.) to off-reef areas. Their abundance, however, increases away from the reefs, as do the numbers of species. Thin-spined forms are also widespread but are seldom found within one mile of reefs. Thick-spined and polyhedral forms occur in off-reef strata. They were found close to reefs, perhaps where currents carried them, in only two cases (north of Redwater and north of Willingdon—see Discussion of Current Patterns). The samples did not cover a sufficient number of wells to obtain adequate information on species distribution. If a more detailed study is made, records of individual species distribution may show that some of them are much more sensitive to environment than are the three growth-form groups.

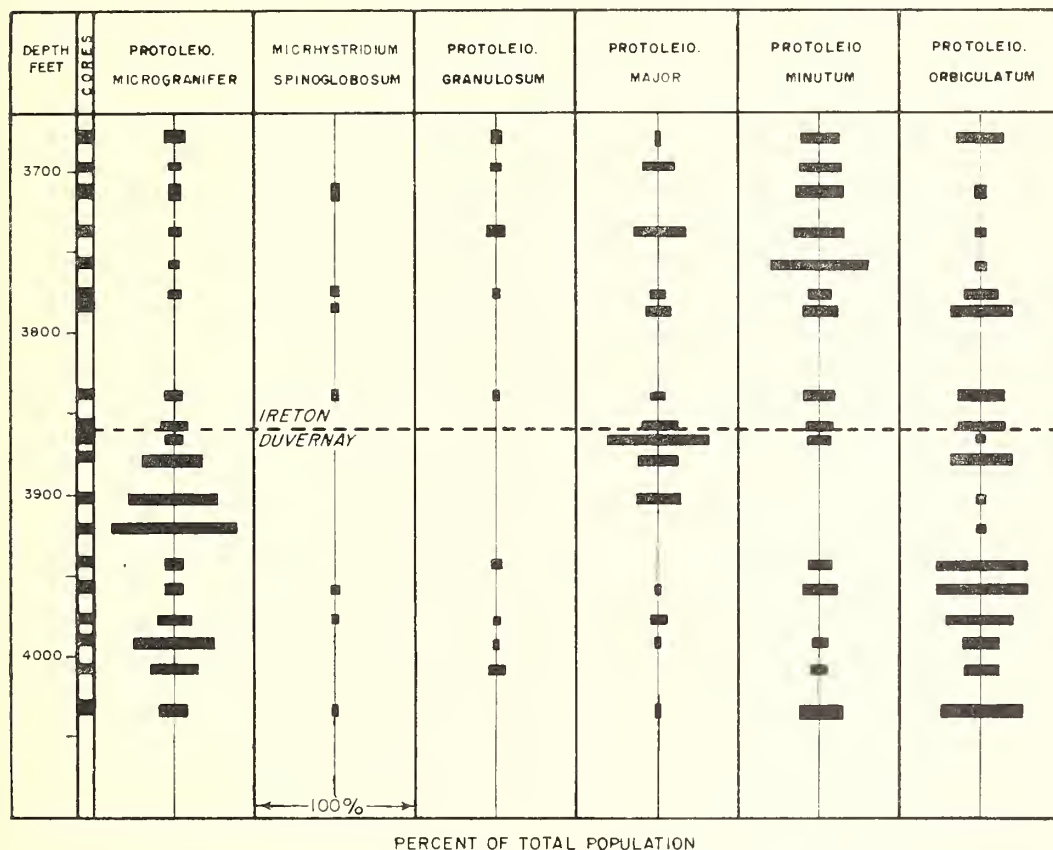


TEXT-FIG. 5. Hystrichospherids on two slides, Anglo-Canadian Beaverhill Lake No. 2. Total curve and selected species.



TEXT-FIG. 6. Hystrichospherids on two slides, A. H. C. and E. Camrose No. 1. Total curve and selected species.

Distribution of plant spores. Abundant plant spores (20 per cent. or more of the total acid-resistant microfossils) are found in the Duvernay member around Redwater reef (text-fig. 8). The percentages increase to the north. Plant spores are moderately abundant north of Township 53 and east of the main reef trend and rare to the south and west of this area. The source of the spores is therefore to the north of the Edmonton area.



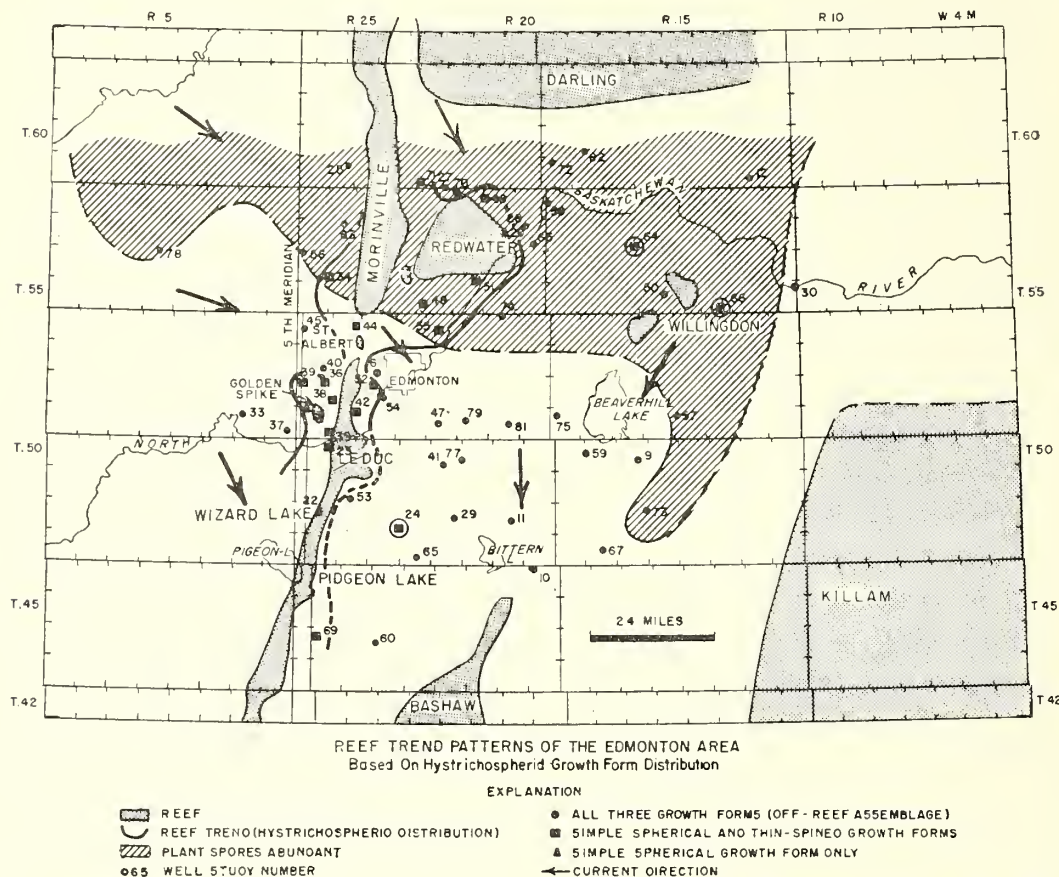
TEXT-FIG. 7. Variations in relative abundance of six selected hystrichospherid species, Anglo-Canadian Beaverhill Lake No. 2.

Water currents were probably most responsible for transporting the spores. Supporting evidence for a northern source is offered by many wells. In part of the Peace River area, the pre-Cambrian surface was emergent during Woodbend time.

Distribution of Chitinozoa. Work done by L. R. Wilson (1955) on the Lower Paleozoic Chitinozoa of the New York area indicates that this group of fossils is most abundant in shallower marine waters, especially near the margins of the basins. For this reason, it is thought that the Chitinozoa of the Duvernay member might indicate proximity to shallower 'platform' areas, on which reefs are more likely to form. The greatest abundance of Chitinozoa in the Duvernay shale is in the area just to the north and

north-east of Redwater reef, to the north and west of Golden Spike reef, and in some wells between the Pigeon Lake and Bashaw reefs (text-fig. 8).

Current configurations. The relative abundance of the plant spores was plotted at each data point. The general pattern for the entire area showed a decrease in abundance to the south and east, but the southward decrease is much less pronounced east of the



TEXT-FIG. 8. Reefs, reef trend patterns, plant spore distribution, and interpreted current directions, Duvernay time. Names of wells and intervals used are given in the list at the end of the paper.

Morinville-Rimbey trend. These gradients in abundance suggest that the major currents were from the north-west and west on the west side of the reef chain, and from the north and north-east on the east side of the reef chain. Andrichuk (1960) came to similar conclusions on the basis of grain size and lithologic studies.

The presence of abundant and varied hystrichospherid assemblages north of Redwater and Willingdon reefs is explained if these current directions are correct, as the small organisms would be carried by the currents and concentrated on the north side of any high on the sea floor.

Further support for the current pattern may be arrived at in another manner.

Runcorn's work on paleomagnetic directions (1956) placed the earth's north pole during Devonian time at approximately 150 degrees east longitude and 35 degrees north latitude. The world distribution of Devonian reefs does not conflict with this interpretation, as they are confined to a broad equatorial belt with relation to this pole. Edmonton, Alberta, would have been at about 20 degrees north latitude. The major oceanic currents against a west-facing land mass at this latitude would have been from the west and north-west. Drag induced on the currents by reef trends, shelves, and land masses would bend them southward, as is the case with currents striking the present west-coast configuration. Currents in shallow-water regions of variable bottom topography are necessarily complex, therefore only major current directions can be suggested.

Reef trends from drilling. The over-all reef trend pattern found by drilling consists of biostromal developments to the north and east of the Edmonton area (Darling and Killam reefs, respectively) and a series of north-south trending barrier-type reefs and subsidiary platform reefs (text-fig. 8). In general, reef development progressed eastward in the Edmonton area during Woodbend time. Reefs east of the Morinville-Rimbey trend grew on Cooking Lake fragmentals; those of the Morinville-Rimbey trend itself have reefal Cooking Lake at their bases; while those to the west started growing during Beaverhill Lake time. The major reef development followed a transgressing sea.

Correlation with hystrichospherid distribution. The reef-trend patterns obtained on the basis of growth-form distribution are shown in text-fig. 8. In most cases, lines drawn about areas where simple and thin-spined growth-forms are present enclose reef trends defined by drilling. In nearly all cases the thick-spined growth-form is found only in off-reef areas.

There are exceptions to this pattern. For example, in the Millet Leduc well (number 24 on text-fig. 8), the off-reef thick-spined hystrichospherids are absent, although drilling has largely eliminated reef possibilities. In other cases, the data were limited by the small number of wells used in the study. Largely for this reason, the Flint-Duhamel reefs and the development at Willingdon are not outlined in text-fig. 8. There are five locations far from known reefs that have only simple and thin-spined growth-forms. These areas (text-fig. 8) are north of Golden Spike (T52, R26, W4th M.), east of Acheson and the northern part of Leduc (T52, R25-26, W4th M.), south of Redwater (T55, R23, W4th M.), the Millet Leduc area (T48, R24, W4th M., Millet Leduc No. 16-6) and around T57, R17, W4th M. (Canadian Superior Kozak No. 16-3). This distribution could indicate shallow water or, in other words, platforms on which reef growth was possible. Chitinozoa and scolecodonts, suggesting shallow water, are common in the first three areas. Two areas that have all three hystrichospherid growth-forms (off-reef assemblages) were found close to reefs. One is just north of Willingdon (T44, R15, W4th M.) at Imperial Willingdon No. 2, and the other is just north of Redwater Reef (T58, R22-23, W4th M.) at Imperial Opal No. 35 and Imperial Egremont West No. 16-36. If currents were from the north in this area, as suggested in the discussion of current patterns, the small hystrichospherids could easily have been carried to these positions on the reef flanks.

Summary. Data presented here show that acid-resistant microfossils can be used to outline broad reef trends and other major sedimentary structures. Because of the large

amount of well control that is required in order to give the pattern any sort of precision, it is doubtful whether the method has immediate practical application to petroleum exploration.

Chitinozoa are generally abundant in areas of relatively coarser sediment. Concentrations of these fossils may help to indicate areas of shallow water where conditions were favourable to reef development. The relative increase in plant spore abundances to the north points toward land masses contemporaneous with the deposition of the Duvernay formation. On the basis of plant spore distribution, major currents to the west of the Leduc-Rimbey reef trend were from the north-west and west, while those to the east of this trend were generally from the north, as a result of southward drag induced by reef configurations and land masses.

SYSTEMATIC SECTION

Classification of hystrichospherids. Most Paleozoic hystrichospherids would fall into the following form categories:

1. Spherical sacs, laevigate to papillate.
 - 1a. Spherical sacs, minor ornamentation, apical pore present.
2. Spherical sacs, apiculate, ciliate, spinose, baculate or pilose, the processes numerous and small in relation to body (vesicle) diameter.
3. Spherical sacs with long simple spines.
4. Spherical sacs with long processes, the tips expanded, branched, dissected or otherwise modified.
5. Roughly spherical sacs with short coarse broad-based apiculae or other structures.
6. Roughly spherical sacs with processes of more than one kind, sometimes with one very large process that lends a bilateral symmetry to the form. Internal structure is apparent on some.
7. Roughly spherical sacs with long processes that are hollow and expanded at the tips to resemble trumpets (almost entirely post-Paleozoic).
8. Lanceolate to fusiform bodies with various types of processes.
9. Reticulate spherical bodies, sometimes with short spinose or pilate processes.
10. Lenticular forms, rectangular to circular, with a thin flange or girdle. Rod-like structures often strengthen the connexion of the flange to the vesicle.
11. Geometrical to saccate forms—triangular and lenticular to tetrahedral and polyhedral, often with long processes at the angles. The processes are broad-based and are an integral part of the vesicle. Some have internal structures.
12. Subspherical to polyhedral forms enveloped in a membrane, the membrane commonly gathered into folds and attached to the vesicle by processes of various kinds.
13. Fusiform bodies.

The species described here belong to groups 1–4 and 9–12. Group 4 is represented only by few species, although it is a characteristic group in the Devonian of eastern North America. Many typical or index species from the eastern Devonian section are lacking in the Alberta assemblages. The reason for this probably lies in the fact that the seaways of the two areas were separate during the Middle Devonian and were not

connected until some time in the Upper Devonian, perhaps too late to allow the more diverse eastern assemblages to migrate into the area of Duvernay-Ireton sedimentation.

Stratigraphic value of hystrichospherids. Published work on hystrichospherids is limited, making it difficult to compare assemblages of different stratigraphic and geographic locations. However, a few generalizations may be drawn on the basis of the scant literature, and control collections from various strata.

Ordovician hystrichospherids are mostly small, the vesicle diameter ranging from 5 to 20 microns for the most part. The most common growth-forms are groups 1 and 2. Groups 3, 4, and 13 are occasional, and forms similar to *Hystrichosphaeridium trispinosum* Eisenack represent group 11.

Silurian hystrichospherids are much more varied, and many are larger in size. Group 4 is very important, containing a number of species of relatively short stratigraphic range. A number of complex forms have processes of more than one type, and some possess bilateral, rather than radial, symmetry. Some possess internal structures. Devonian forms are similar to those of the Silurian, but many species are different. The polyhedral or geometrically shaped group, with processes broad-based and an integral part of the vesicle, is relatively more important, and species with the spines arranged in one plane or with stubby complex spines are also more prevalent. Deunff (1954, 1957), Radforth and McGregor (1954), White (1862), and theses prepared at the University of Massachusetts under L. R. Wilson, illustrate a few of the Siluro-Devonian hystrichospherids of eastern Canada and New York.

Upper Paleozoic forms are poorly known. Groups 5 to 6 and 8 are important but most of the others are present also. During the Permian, small forms of group 2 seem to be predominant, at least in the area from the north-western States to Alaska. Small triangular to tetrahedral rectangular forms of group 11 are common. Many of the same polyhedral forms are present in the Triassic sediments of western Canada, some with the single flagellum of certain chrysophyte swimmers in possibly fresh to brackish water deposits (J. Jansonius, study in progress). In the Permian rocks we also find the first hystrichospherids of known dinophycean affinities.

Nomenclatural considerations. The majority of Paleozoic hystrichospheres and leiospheres have been apportioned to the genera *Leiosphaeridia* Eisenack 1958, *Tasmanites* Newton 1875, *Micrhystridium* Deflandre 1937, *Baltisphaeridium* Eisenack 1958, *Veryhachium* Deunff 1954, *Cynatiophaera* O. Wetzel 1933, *Dictyotidium* Eisenack 1955, and *Leiofusa* Eisenack 1938. Our knowledge of these forms is still small, and it is fortunate that so few genera have been proposed. A number of changes are now necessary. Timofeev (1959) has proposed several genera based on the type of ornamentation for leiospheres without pylom or canals. *Protoleiosphaeridium* (type species cited as *P. conghintinatum* in his 1960 paper) includes laevigate to shagreen (finely granulose) species and is here slightly expanded to include papillate and minutely spinulose forms. Many of these small leiospheres were formerly assigned to *Leiosphaera* Eisenack 1938. In 1951 Eisenack accepted the fact that the type species, *L. solida*, was similar to and possibly conspecific with *Sporangites huronensis* Dawson, following Krausel's work of 1941. Eisenack later (1958a) completed the transfer of *L. solida* to *Tasmanites huronensis* (Dawson). *Leiosphaeridia* was proposed by Eisenack (1958a) for thin-walled forms formerly included in *Leiosphaera*. However, the generic description clearly states that a pylom is present

(page 3). The inclusion of the many small aporate spheres without pylom within the pylom-bearing genus *Leiosphaeridia* is unsatisfactory from stratigraphic and taxonomic standpoints, and the acceptance of *Protoleiosphaeridium* is recommended.

Micrhystridium Deflandre 1937 was defined with a maximum size of 20 microns. A number of species have size limits that extend above and below this arbitrary limit, and many species averaging over 20 microns have no other characteristic to distinguish them from smaller species. Most of these larger forms were originally assigned to *Hystrichosphaeridium* Deflandre 1937. Eisenack (1958b) proposed some important changes. *Hystrichosphaeridium* was restricted to forms with open-tipped spines similar to the type species, *H. tubiferum* (Ehrenberg) Deflandre, from the Mesozoic. *Baltisphaeridium* (ex *Hystrichosphaeridium*) was proposed for species with closed-tip spines. No revision was made of *Micrhystridium*. As of that date, *Micrhystridium* stood for species under 20 microns in size, with closed-tip spines of various kinds, and *Baltisphaeridium* included larger forms of similar type.

The type of *Micrhystridium*, *M. inconspicuum* (Deflandre) Deflandre 1937, has simple spines, all of one kind. The original illustration of the type of *Baltisphaeridium*, *B. longispinosum* (Eisenack 1931) shows a form with simple spines. In later papers, Eisenack (1938, 1951) placed in the species a number of specimens with forked spines, broad processes with constricted bases, and other types. He characterized illustrations of simple forms, however, as '... recht typische Stücke mit sehr langer und fast fadenförmigen Anhängen'. The true type of *Baltisphaeridium* is therefore morphologically similar to that of *Micrhystridium*, and overlap of the simply spined species is inevitable. *Micrhystridium* is here emended to include only simply spined forms, the spines closed at the tips and generally uniform in structure. The size limit of 20 microns is removed. The type species of *Baltisphaeridium* is considered as a species of *Micrhystridium* emend., and the genus abandoned. *Multiplicisphaeridium* new genus is proposed for species that possess forked or otherwise modified processes with closed tips, the processes generally uniform within a single species. No size limits are imposed. Formal reassignment of previously described species to these new or emended genera are not made here in order to avoid the problems of synonymy that would arise if these proposals are not generally accepted.

Veryhachium Deunff 1954 was proposed for more or less polyhedral (triangular to prismatic) forms with broad-based processes. The type species *V. trisulcun* (Deunff) was not described until 1959, although it had been illustrated (1951, 1954). A holotype and paratypes are listed with the description, and the genus is now considered to be properly validated. The concept of *Dictyotidium* is broadened slightly to include additional reticulate species, but the basic diagnosis is not changed. *Cymatiosphaera* is suitable for most Paleozoic species with enveloping membranes that are gathered into various reticulate patterns and stiffened by spine-like radial processes.

Other new hystrichosphere genera proposed are *Duvernaysphaera* and *Paleopedicystus*. A new type of acid-resistant microfossil is described under the name *Hoegisphaera* n. gen., new chitinozoan structures are illustrated, and a species of *Tasmanites* is described.

Many species of hystrichospherids are broadly defined and interpreted at this time, and much variation is allowed. The author believes that with further work many of these species will be separated into two or more distinct entities, with little overlap. The Upper Devonian hystrichospherids of western Canada are relatively constant in form, the

variation being confined to slight differences in the number of spines or in the ratio of spine length to vesicle diameter.

Type specimens are available for study in the permanent collections of Imperial Oil Limited, 300 Ninth Avenue W., Calgary, Canada.

HYSTRICHOSPHERE GROUP

Genus PROTOLEIOSPHAERIDIUM Timofeev 1959

Type species. P. conglutinatum Timofeev 1959.

Revised diagnosis. Vesicle ellipsoidal to spherical; wall thin, aporate; canals absent; pylom absent; ornamentation absent or minor, including granules, papillae and small short spinules.

Remarks. The description given by Timofeev is expanded to include other types of minor overall ornamentation besides laevigate and shagreen. The change is not sufficiently important to warrant citation as a formal emendation. *P. cambriense* should be excluded from the genus, as it possesses characteristics not covered in the generic description. *P. nervatum* perhaps belongs to *Dictyotidium*.

Protoleiosphaeridium minutum sp. nov.

Plate 48, fig. 3

Holotype. Imperial Willingdon No. 2, Duvernay member, 2,975–3,050' composited decontaminated cuttings. Slide 1, 47.5 109.2; 18 microns.

Diagnosis. Vesicle circular, laevigate, thin-walled; frequently folded; diameter 12–20 microns.

Remarks. Smooth sacs of similar appearance are present in many marine Paleozoic rocks.

Protoleiosphaeridium orbiculatum sp. nov.

Plate 48, fig. 12

Holotype. Imperial Willingdon No. 2, Duvernay member, 2,975–3,050' composited decontaminated cuttings. Slide 1, 38.2 124.5; 40 microns.

Diagnosis. Vesicle circular, smooth, frequently folded, relatively thick-walled for the genus; diameter 24–48 microns.

Remarks. Abundant to frequent in the Woodbend and Beaverhill Lake formations. Wall thicker than *Leiosphaeridia wenlockia* Downie 1959.

Protoleiosphaeridium microgranifer sp. nov.

Plate 48, fig. 4

Holotype. Imperial Willingdon No. 2, 11-20-55-15W4th M., 2,975–3,050' composited decontaminated Duvernay cuttings. Slide 1, 39.8 121.5; 31 microns.

Diagnosis. Vesicle circular, microgranulose, commonly folded; diameter 35–45 microns.

Remarks. *A. granulosa* has distinct granules slightly more than 0.5 microns in diameter, whereas the granules in this species are near the limit of resolution of the microscope.

Protoliosphaeridium major sp. nov.

Plate 48, fig. 6

Holotype. Imperial *et al.* Faust South 6-2, 6-2-72-11W5th. M., Beaverhill Lake fm., 6,750-5' core. Slide 2, 31.5 120.2; 60 microns.

Diagnosis. Vesicle circular; laevigate; relatively thick-walled, folding occasional; size 55-85 microns.

Protoliosphaeridium diaphanum sp. nov.

Plate 48, fig. 8

Holotype. Imperial Spruce Grove No. 1, 4-25-52-27W4th M., picked Duvernay cuttings, 6,065-120'. Slide 1, 34.7 110.9; 48 microns.

Diagnosis. Vesicle circular; surface minutely granulose, separation of granules 1-2 microns; wall very thin, folding common; diameter 40-50 microns.

Remarks. Granules are finer and the wall much thinner than in *P. granulosum* n. sp. The compound folding of the vesicle wall is a characteristic feature of the species.

Protoliosphaeridium granulosum sp. nov.

Plate 48, fig. 1

Holotype. A. C. Beaverhill Lake No. 2, 11-11-50-17W4th M., Duvernay member, 4,030' core. Slide 1, 31.9 120.2; 28 microns.

Diagnosis. Vesicle circular; densely and evenly granulose, granules rounded, one micron or less separation; minor folding common; diameter 16-28 microns.

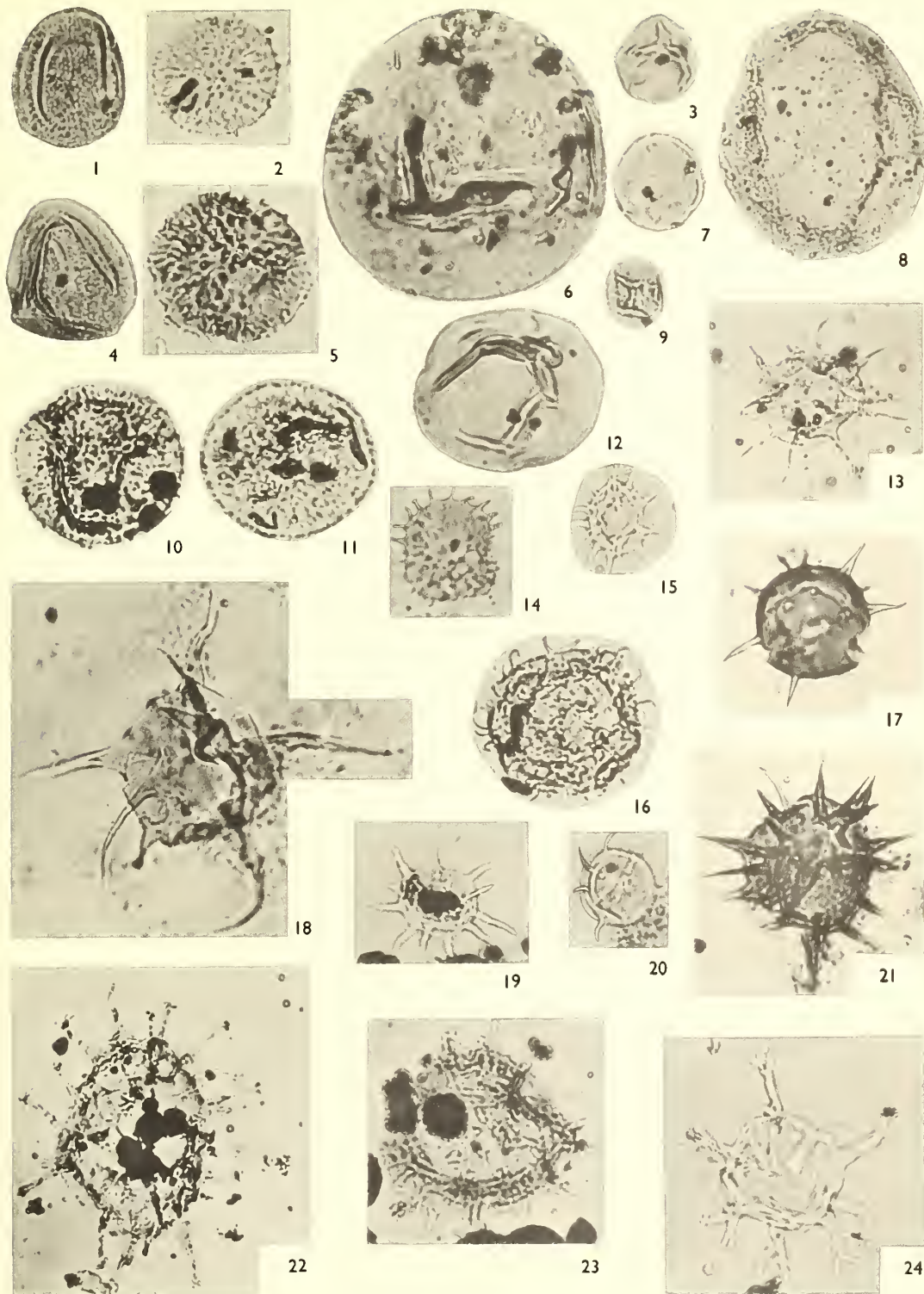
Protoliosphaeridium papillatum sp. nov.

Plate 48, figs. 10-11

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Ireton member, 5,238' core. Slide 1, 42.7 111; 36 microns (fig. 10). Illustrated: same well, Ireton member, 5,142' core, Slide A, 42.7 122.8; 35 microns.

EXPLANATION OF PLATE 48

- Figs. 1-12. *Protoliosphaeridium* spp. 1, *P. granulosum* sp. nov., holotype, 28 microns. 2, 5, *P. microsaetosum* sp. nov. 2, 27 microns. 5, Holotype, 33 microns. 3, *P. minutum* sp. nov., holotype, 18 microns. 4, *P. microgranifer* sp. nov., holotype, 31 microns. 6, *P. major* sp. nov., holotype, 60 microns. 7, *P. cryptogranulosum* sp. nov., holotype, 20 microns. 8, *P. diaphanum* sp. nov., holotype, 48 microns. 9, *P. parvigranulosum* sp. nov., holotype, 14.5 microns. 10, 11, *P. papillatum* sp. nov. 10, Holotype, 36 microns. 11, 35 microns. 12, *P. orbiculatum* sp. nov., holotype, 40 microns.
- Figs. 13-21. *Micrhystridium* spp. 13, *M. vigintispinum* sp. nov., holotype, vesicle 24 microns. 14, *M. echinosum* sp. nov., holotype, vesicle 21 microns. 15, *M. bistchoensis* sp. nov., holotype, vesicle about 17 microns. 16, *M. breviciliatum* sp. nov., holotype, vesicle 34 microns. 17, *M. spinoglobosum* sp. nov., holotype, vesicle 24 microns. 18, *M. octospinosum* sp. nov., holotype, vesicle 33 microns. 19, *M. albertensis* sp. nov., holotype, vesicle 18 microns. 20, *M. angustum* sp. nov., holotype, vesicle 15 microns. 21, *M. crassiechinatum* sp. nov., holotype, vesicle 30 microns.
- Figs. 22-24. *Multiplicisphaeridium* spp. 22, *M. ? sprucegrovensis* sp. nov., vesicle 42 microns. 23, *M. truncatum* sp. nov., holotype, vesicle 38 microns. 24, *M. ramispinosum* sp. nov., holotype, vesicle 29 microns.



Diagnosis. Vesicle circular; densely papillate, papillae short, variable in size, shape and spacing, height 0·8–1·3 microns; diameter 24–38 microns.

Remarks. *Baltisphaeridium microspinosum* (Eisenack) in Downie, 1959, is larger and seemingly more densely papillate.

Protoleiosphaeridium microsaetosum sp. nov.

Plate 48, figs. 2, 5

Holotype. Cal. Std. Winterburn Prov. No. 1, 10-4-53-25W4th M., 5,535' core, Duvernay member. Slide 1, 40·9 113·5; 33 microns (fig. 5). Illustrated: same sample, Slide 1, 44·3 110·5; 27 microns.

Diagnosis. Vesicle circular; saetose, spines crowded, tubular, 2–4 microns long, tips rounded, separation about 2 microns; diameter 25–44 microns, often appears ragged.

Remarks. Longer spines than *P. papiliatum*.

Protoleiosphaeridium cryptogranulosum sp. nov.

Plate 48, fig. 7

Holotype. Imperial Willingdon No. 2, 11-20-55-15W4th M., Duvernay member, picked composited cuttings, 2,975–3,050'. Slide 1, 43·3 109; 20 microns.

Diagnosis. Vesicle spherical-ellipsoidal; microgranulose, granules variable in size and spacing, separation 1–3 microns; size 17–20 microns.

Protoleiosphaeridium parvigranulosum sp. nov.

Plate 48, fig. 9

Holotype. Imperial Willingdon No. 2, 11-20-55-15W4th M., Duvernay member, picked composited cuttings, 2,975–3,050'. Slide 1, 46·3 112·4; 14·5 microns.

Diagnosis. Vesicle circular in outline; densely covered with minute granules that in part tend toward a tubular shape, one micron long at most, separation not over 1·5 microns; 13–16 micron size range.

Genus *LEIOSPHAERIDIUM* Timofeev 1959 emend.

Type species. *L. eisenackii* Timofeev 1959.

Emended diagnosis. Vesicle circular in outline; large (100–300 microns and larger); laevigate; wall thin to moderate in thickness, aporate, without canals; folding minor to prominent, commonly taper-point in thin-walled spherical species.

Remarks. Timofeev (1959) cited the genus as *Leiosphaeridium* Eisenack 1938 emend. Timofeev. The alteration of *Leiosphaera* to *Leiosphaeridium* is not valid. The name is here regarded as a new generic taxon. The original description by Timofeev (1959), 'vesicle thick with smooth surface', is correct only in comparison with *Protoleiosphaeridium*, as the wall is thin in comparison with *Tasmanites* of *huronensis* type. Timofeev proposed the names *Trachysphaeridium* and *Lophosphaeridium* for finely granulose (shagreen) and tuberculose species.

Leiosphaeridium fastigatirugosum sp. nov.

Plate 50, fig. 9

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Ireton member, 5,354' core. Slide 1, 38·8 123·2; 125 microns.

Diagnosis. Body spherical; laevigate; wall structureless, relatively thin; compression accompanied by the formation of taper-point folds; size 120–150 microns and perhaps larger.

Remarks. Much larger similar specimens may or may not belong to this species. No 'pylom' could be demonstrated. Species described by Timofeev that have taper-point folds are all shagreen.

Genus *MICRHYSTRIDIUM* (Deflandre) emend.1937 *Micrhystridium* Deflandre, pp. 79–80.

Genotype. *Micrhystridium inconspicuum* (Defl.) Defl. 1937.

Description. Vesicle subspherical to spherical; spinose, spines simple, generally uniform, numerous, their bases sometimes arranged in a subpolygonal pattern, tapering to tubular, tips closed.

Remarks. The upper size restriction is removed. Forms with forked or otherwise differentiated appendages are placed in *Multiplicisphaeridium* n. gen. Forms with distinct ridges defining polygonal areas are placed in *Dictyotidium*. Small polyhedral to asterate forms, the appendages an integral part of the vesicle, are considered species of *Veryhachium* Deunff.

Micrhystridium breviciliatum sp. nov.

Plate 48, fig. 16

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Duvernay member, 5,625' core. Slide 8, 32·9 120·2; vesicle 34 microns.

Diagnosis. Vesicle circular in outline; densely ciliate, length of cilia about 3·4–4 microns, separation about 4 microns, tubular in shape with rounded tips, often curved; vesicle 32–37 microns.

Micrhystridium echinosum sp. nov.

Plate 48, fig. 14

Holotype. Calmont Std. Winterburn Province No. 1, 10-4-53-25W4th M., Ireton member, 5,375' core. Slide 1, 40·8 120·3; vesicle 21 microns.

Diagnosis. Vesicle subcircular; echinate, spines approximately 4 microns long, less than 1 micron in diameter, about 2–4 microns apart, spine tips rounded or faintly enlarged (compressional?); vesicle 17–22 microns.

Remarks. The vesicle is smaller and the spines closer together than in *M. breviciliatum* n.sp.

Micrhystridium angustum sp. nov.

Plate 48, fig. 20

Holotype. Texaco (Shaw) Spruce Grove No. 1, 4-11-53-27W4th M., picked composited Duvernay cuttings, 5,915-90'. Slide 3, 40 109-6; vesicle 15 microns.

Diagnosis. Vesicle circular; processes ciliate, 3-5 microns long, tips pointed, 15-17 in number, evenly disposed; vesicle size 14-16 microns.

Remarks. *Micrhystridium bacilliferum* Deflandre 1946 is smaller and has a larger number of spines. *Hystriosphæridium* cf. *brevispinosum nanum* Defl. 1945 is twice the diameter of this species and has more spines.

Micrhystridium spinoglobosum sp. nov.

Plate 48, fig. 17

Holotype. Imperial Duvernay No 1, 6-30-55-11W4th M., 2,245-8' core, Duvernay member. Slide 1, 48 111; vesicle 24 microns.

Diagnosis. Vesicle spherical; spinose, spines 12-18 in number, 6-9 microns long and 2 microns wide at base, spike-shaped and sharply pointed; vesicle size 17-24 microns.

Remarks. *M. inconspicuum* (Deflandre) Deflandre 1937 is much smaller and has a thicker wall. *M. parinconspicuum* Deflandre 1945 (Silurian) has a diameter of 10-15 microns and possibly a larger number of spines. Frequent.

Micrhystridium bistchoensis sp. nov.

Plate 48, fig. 15

Holotype. Imperial Bistcho Lake 7-7, 7-7-124-2W6th M., Beaverhill Lake (?) equivalent, 4,906' core. Slide 3, 30 111-3; 24 microns overall, vesicle about 17 microns, spine length about 6 microns.

Diagnosis. Vesicle subspherical; laevigate; spines broad-based but taper rapidly to tubular processes with pointed tips, about twenty in number, length approximately one-third vesicle diameter; overall size 20-26 microns.

Micrhystridium vigintispinum sp. nov.

Plate 48, fig. 13

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Duvernay member, 5,546' core. Slide 1, 41-6 114; vesicle 24 microns, spines 12 microns, overall size 40 microns.

Diagnosis. Vesicle subspherical-ellipsoidal; laevigate; spines narrow, tapered to fine ciliate tips, basal diameter about 1.5 microns, length about half vesicle diameter, about 20 in number; overall size about 40 microns.

Micrhystridium albertensis sp. nov.

Plate 48, fig. 19

Holotype. Imperial Bistcho Lake 7-7, 7-7-124-2W6th M., Beaverhill Lake (?) equivalent, 4,906-11' core. Slide 1, 40 112; vesicle 18 microns, spines 10-11 microns.

Diagnosis. Vesicle subspherical; laevigate; spinose, spines simple, tapering, 13-14 in number, length half to five-eighths vesicle diameter; vesicle diameter 16-19 microns.

Micrhystridium octospinosum sp. nov.

Plate 48, fig. 18

Holotype. Imperial Egremont West No. 6-36, 6-36-58-23W4th M., composited Duvernay core, 3,948–4,008'. Slide 1, 48 116; vesicle 33 microns, spines about 24 microns.

Diagnosis. Vesicle roughly spherical; appendages eight in number, broad-based, tentacle-like, tips pointed, length 20–28 microns, width at base about 4–5 microns; folding common; vesicle diameter 24–33 microns.

Remarks. Number of spines constant. The polyhedral shape characteristic of *Veryhachium* is absent. *Hystichosphaeridium spiciferum* Deunff 1955 has up to fifteen appendages that are longer than those of this species.

Micrhystridium duvernayensis sp. nov.

Plate 49, fig. 8

Holotype. A. C. Beaverhill Lake No. 2, 11-11-50-17W4th M., Duvernay member, 3,988' core. Slide 1, 45·3 110; vesicle 40 microns.

Diagnosis. Vesicle circular; spines ciliate, about twenty in number, 10–12 microns long, tips pointed; vesicle wall thin; vesicle diameter 35–40 microns.

Remarks. The wide separation of the spines characterizes this species.

Micrhystridium crassiechinatum sp. nov.

Plate 48, fig. 21

Holotype. Bear Rodeo No. 1, 8-20-89-9W4th M., 471–81' core, Beaverhill Lake fm. Slide 8, 37·4 117; vesicle 30 microns.

Diagnosis. Vesicle subcircular in outline; sub-spherical; spines long, straight, tapering to a sharp point, about twenty-two in number, length 10–15 microns; vesicle diameter 24–33 microns.

Remarks. The stiff, straight habit of the spines characterizes this species.

Genus MULTIPLICISPHAERIDIUM gen. nov.

Text-fig. 9e

Type species. *Multiplicisphaeridium ramispinosum* sp. nov.

Diagnosis. Vesicle ellipsoidal to spherical; processes separate, narrow-based, tips multifurcate, expanded, dissected or otherwise modified but not open; processes all of one type or variations of one type, not differentiated into distinctive orders or kinds of processes; wall surface exclusive of processes laevigate to finely granulose.

Remarks. All species with simple unmodified spine tips are referred to *Micrhystridium* emend. All species with broad-based processes that are an integral part of the vesicle shape are referred to *Veryhachium* Deunff. A new genus should be proposed for species with more than one order of processes, i.e. the different types of processes are distinct and have a constant spatial relationship to each other.

Multiplicisphaeridium truncatum sp. nov.

Plate 48, fig. 23; text-fig. 9f

Holotype. Imperial Paddle River No. 1, 5-17-56-8W5th M., Duvernay-Cooking Lake equivalent, 7,930-2' core. Slide A, 38·7 124·6; vesicle 38 microns.

Diagnosis. Vesicle circular to egg-shaped; processes crowded, ciliate, approximately 8 microns long, seemingly set on low pedestals (compressional feature), spine tips pilose to bifurcate on the same specimen, spine separation about 3 microns; vesicle size 28-38 microns.

Remarks. *H. hirsutoides* Eisenack 1951 is larger (75-80 microns) and seems to have shorter processes.

Multiplicisphaeridium? sprucegrovensis sp. nov.

Plate 48, fig. 22, Plate 49, fig. 6; text-fig. 9j

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Duvernay member, 5,635' core. Slide 3, 39·3 112·8; vesicle diameter 36 microns, processes 16 microns (Pl. 49, fig. 6). Illustrated: Imperial Paddle River No. 1, 5-7-56-8W5th M., Duvernay-Cooking Lake equivalent, 7,823-8' core. Slide 1, 41·4 113·3; vesicle 42 microns maximum, spines about 13 microns.

Diagnosis. Vesicle circular; processes crowded, 10-16 microns long, 2 microns wide at base but tapering to about 1 micron near tips, tips enlarged and tetrafurcate, secondary tips 2-4 microns long; appendage separation 3-4 microns; vesicle diameter 35-44 microns.

Remarks. About twenty-five to thirty processes extend beyond the vesicle margin. The closed nature of the tips could not be definitely determined, even with oil immersion, and the assignment is therefore provisional.

Multiplicisphaeridium ramispinosum sp. nov.

Plate 48, fig. 24; text-fig. 9g-h

Holotype. Imperial Bistcho Lake No. 7-7, 7-7-124-2W6th M., Woodbend fm., 4,159-64' core. Slide 5, 41·5 117·6; vesicle 29 microns.

Diagnosis. Vesicle subcircular; processes generally bifurcate, each branch again bifurcate or trifurcate, tips multiple; processes usually twelve in number, 10-15 microns long; vesicle size 19-29 microns.

Remarks. Processes variable. A much larger similar species has been described from Baltic Silurian sediments (240 microns; Eisenack 1938, pl. 4, figs. 3-5). *Hystrichosphaeridium ramusculosum* Defl. 1945 has some simple pointed processes and may be a species with two distinct orders of processes.

Multiplicisphaeridium spicatum sp. nov.

Plate 49, fig. 21; text-fig. 9i

Holotype. Imperial Willingdon No. 2, 11-20-55-15W4th M., picked composited Duvernay cuttings, 2,975-3,050'. Slide 1, 34·7 112·6; vesicle 65 microns.

Diagnosis. Vesicle circular in outline; processes densely crowded, 6–9 microns long, $1\frac{1}{2}$ –2 microns wide, cylindrical, mostly bifurcate; size 63–72 microns.

Remarks. *H. ex aff. multipilosum* Eisenack 1938 (pl. 3, fig. 9) from the Silurian has finer processes.

Genus VERYHACHIUM Deunff 1954

Type species. *Veryhachium trisulcum* (Deunff) Deunff 1959.

Description. Shape extended polyhedral; appendages an integral part of the vesicle, hollow, tips closed, usually long but short in some species.

Remarks. The type species was not described until 1959, although illustrated and given a new combination with the generic proposal in 1954.

Veryhachium brevitrispinum sp. nov.

Plate 49, fig. 1

Holotype. A. C. Beaverhill Lake No. 2, 11-11-50-17W4th M., Duvernay member, 3,988' core. Slide 1, 38-1 118-2; size (centre of one side to tip of opposing spine) 29 microns.

Diagnosis. Outline convexly trigonal; appendages at each corner, broad-based, tapered rapidly to a point, sometimes curved, short for the genus; vesicle wall minutely granulose (oil); size measured from centre of one side to tip of opposing appendage, 24–32 microns.

Remarks. Granulose surface and short spine length distinguish this species from *Hystrichosphaeridium trispinosum* Eisenack 1938. No internal structures are present. *V. trisulcum* var. *reductum* Deunff 1959 is laevigate.

EXPLANATION OF PLATE 49

Figs. 1–5, *Veryhachium* spp. 1, *V. brevitrispinum* sp. nov., holotype, 30 microns overall. 2, 5, *V. sp. cf. H. trispinosum* Eisenack. 2, 30 microns, one side to opposing spine tip. 5, 36 microns, one side to opposing spine tip. 3–4, *V. octoaster* sp. nov., 3, Holotype, 54 microns overall. 4, 38×40 microns overall.

Fig. 6, *Multiplicisphaeridium? sprucegrovensis* sp. nov., holotype, vesicle 36 microns.

Fig. 7, *Veryhachium duodeciaster* sp. nov., holotype, 45 microns overall.

Fig. 8, *Michrystidium duvernayensis* sp. nov., holotype, vesicle 40 microns.

Fig. 9, *Veryhachium minor* sp. nov., holotype, 24 microns overall.

Figs. 10, 11, *Duvernaysphaera tenuicingulata* sp. nov. 10, Holotype, vesicle 32 microns. 11, Vesicle 31 microns.

Fig. 12, *Veryhachium sedecimspinosum* sp. nov., holotype, 21 microns overall.

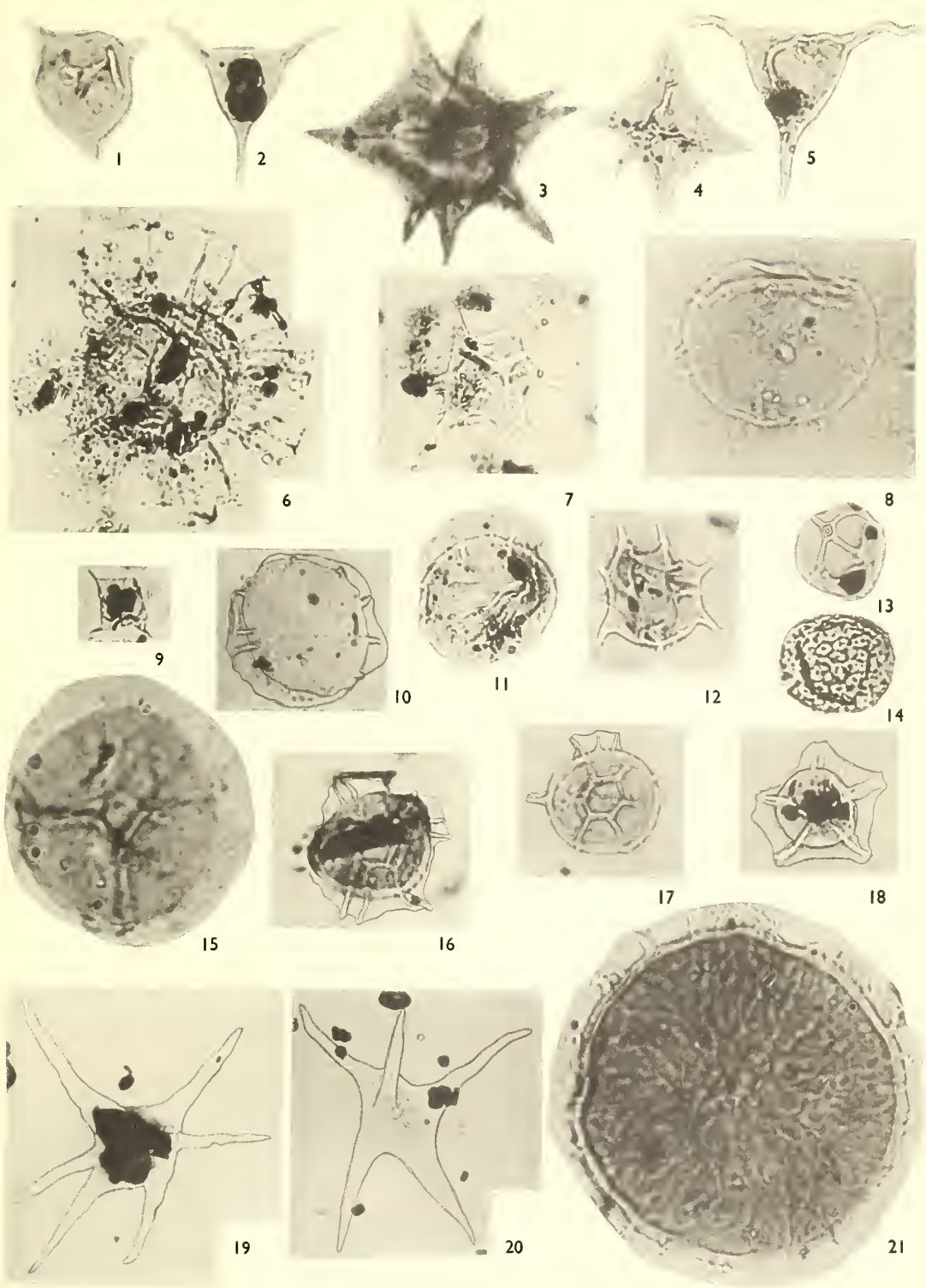
Figs. 13, 14, *Dictyotidium* spp. 13, *D. polysymmetrium* sp. nov., holotype, 21 microns. 14, *D. polygonium* sp. nov., holotype, 29 microns (lower magnification than fig. 13).

Figs. 15–18, *Cymatiosphaera* spp. 15, *C. tetraster* sp. nov., holotype, vesicle 20 microns (oil). 16–17, *C. perimembrana* sp. nov. 16, Holotype, vesicle 28 microns. 17, Vesicle 24 microns. 18, *C. pentaster* sp. nov., holotype, 29 microns overall, vesicle 18 microns.

Fig. 19, *Veryhachium polyaster* sp. nov., var. *hexaster* var. nov., type, 72 microns overall.

Fig. 20, *Veryhachium polyaster* sp. nov., holotype, 60 microns overall.

Fig. 21, *Multiplicisphaeridium spicatum* sp. nov., holotype, vesicle 65 microns.



STAPLIN, Upper Devonian hystrichspherids

Veryhachium sp. cf. *H. trispinosum* Eisenack

Plate 49, figs. 2, 5

1938 *Hystichosphaeridium trispinosum* Eisenack, 14, 16, text-figs. 2-3.

Description. Variable, sides of vesicle almost straight, size from centre of one side to tip of opposing appendage, 24-38 microns. No internal rods or structures. Laevigate.

Remarks. Species of this general shape range from Ordovician to Recent, but some have characteristics that enable them to be used in age determinations. A minute structure interpreted as a single flagellar sheath is present on some Triassic forms, providing a resemblance to the swarmer of *Phaeodermatium* (filamentous chrysophyte). The genus very likely includes representatives of several groups.

Figured specimen. Imp. Paddle River No. 1, 5-17-56-8W5th M., 7,519' core, Lower Ireton member. Slide 6, 38.5 127.3; centre of one side to tip of opposing spine 36 microns (fig. 5). Imperial Bistcho Lake 7-7, 7-7-124-2W6 M., 4,906-11' core, Beaverhill Lake? equivalent. Slide 1, 33.4 125.7; 30 microns, centre of one side to tip of opposing spine.

Veryhachium polyaster sp. nov.

Plate 49, fig. 20

Holotype. Imp. Bistcho Lake 7-7, 7-7-124-2W6th M., Beaverhill Lake? fm., 4,906-11' core. Slide 1, 18.7 120.8; overall size about 60 microns, vesicle central area approx. 18 microns.

Diagnosis. Vesicle polyhedral, composed of central area and five long tapering appendages; appendages an integral part of the whole, broad-based, not arising in the same plane; laevigate; overall size 60-70 microns.

Veryhachium polyaster sp. nov., var. *hexaster* var. nov.

Plate 49, fig. 19

Holotype. Imp. Bistcho Lake 7-7, 7-7-124-2W6th M., Beaverhill Lake? fm., 4,906-11' core. Slide 1, 25.9 124.1; overall size 72 microns.

Diagnosis. Vesicle polyhedral, composed of central area and six long tapering appendages, the appendages are broad-based and are an integral part of the whole, not arising in the same plane; laevigate; overall size 60-75 microns.

Remarks. Forms with five and six appendages occur together and seem to represent the same species. The appendages are tapered and pointed, unlike *Veryhachium hebetatum* Deunff 1957.

Veryhachium octoaster sp. nov.

Plate 49, figs. 3-4

Holotype. Imperial Leduc No. 253, 11-13-50-27W4th M., Ireton member, 5,515' core. Slide 2, 41.2 114.3; overall size 54 microns (fig. 3). Illustrated—Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., 5,118' core, Lower Ireton member. Slide A, 36.3 117; 38×40 microns overall dimensions.

Diagnosis. Vesicle irregularly polyhedral, star-shaped in outline, with eight broad-based appendages that are an integral part of the whole, appendages not arising in the same plane, tips bluntly pointed, dark thin lines radiating from the central part of the

vesicle to the tips of the projections sometimes visible; laevigate to faintly roughened; overall size 35–55 microns.

Remarks. *V. balticum* (Eisenack 1951) has an overall size of 80–85 microns, and some specimens have bifurcate appendage tips. *H. oligospinosum* (Eisenack 1934) is much larger. *Xanthidium* sp. White 1862 (p. 386, figs. 7–8) from the Silurian Lockport fm. closely resembles *V. octoaster* n. sp. *V. exasperatum* Deunff 1955 is much larger, the spine tips are broader, and the thin fibres are missing. Occasional specimens with six or seven processes have been found.

Veryhachium minor sp. nov.

Plate 49, fig. 9

Holotype. Imperial Bistcho Lake 7-7, 7-7-124-2W6th M., Beaverhill Lake? equivalent, 4,906–11' core. Slide 1, 20.4 121.9; 24 microns overall.

Diagnosis. Vesicle polyhedral, generally compressed to a subquadrate outline; five appendages, integral parts of the body, rapidly tapered to sharp points, one often not visible due to folding; laevigate; size 20–28 microns.

Remarks. This small species has fewer appendages than *Veryhachium polyaster* n. sp. *V. minutum* Downie 1958 has four or six appendages and is smaller.

Veryhachium duodeciaster sp. nov.

Plate 49, fig. 7

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Duvernay–Cooking Lake equivalent, 5,605' core. Slide A, 36.6 112.3; 45 microns, central portion roughly 18 microns.

Diagnosis. Vesicle subspherical-polyhedral; laevigate; appendages broad-based, an integral part of the vesicle, tapering to fine tentacle-like spines, twelve in number; overall size about 45 microns.

Remarks. Spines are more broadly based than on the specimens referred to *Micrhystridium stellatum* Deflandre by Downie 1959.

Veryhachium sedecimspinosum sp. nov.

Plate 49, fig. 12

Holotype. Imperial Willingdon No. 2, 11-20-55-15W4th M., 2,975–3,050', picked composited Duvernay cuttings. Slide 1, 39.6 113.8; 21 microns overall, spines about 6 microns.

Diagnosis. Vesicle polyhedral-subsppherical; processes broad-based, an integral part of the vesicle, fifteen–sixteen in number; laevigate; size 19–25 microns.

Remarks. This species is almost transitional between *Veryhachium* and *Micrhystridium*.

Genus DUVERNAYSPHAERA gen. nov.

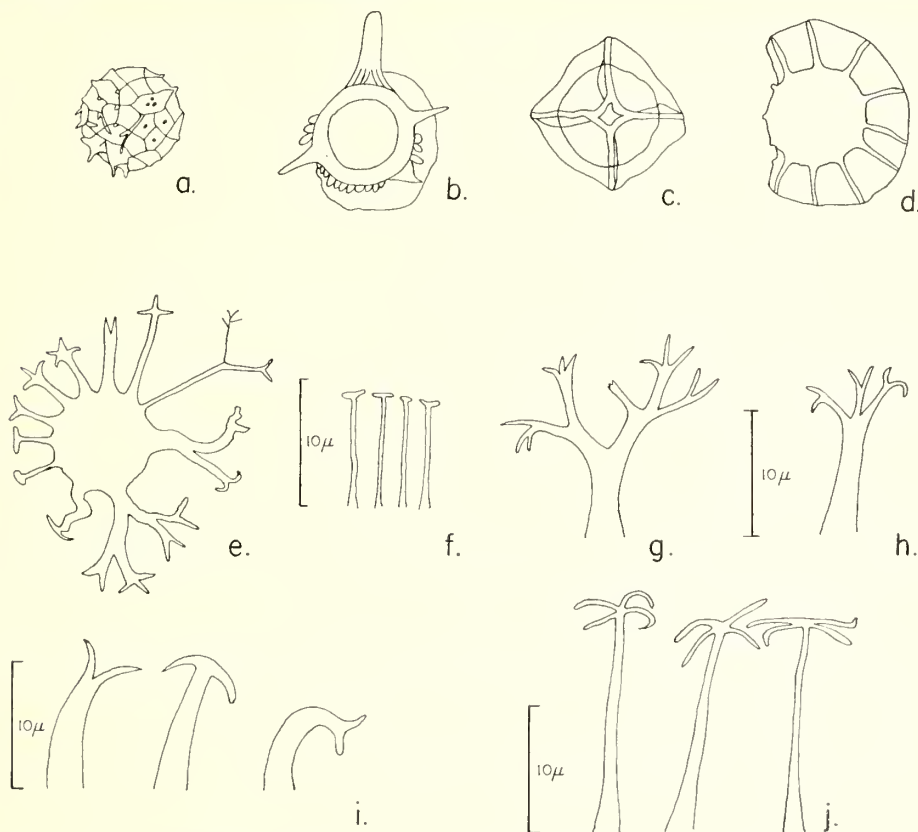
Text-fig. 9d

Type species. *Duvernaysphaera tenuicingulata* sp. nov.

Diagnosis. Vesicle circular in outline, surrounded by an appressed diaphanous membrane

that extends beyond the vesicle margin as a flange, the flange supported by simple rods or spokes arising from the vesicle that are present only in the equatorial plane, much like the fin of a fish.

Remarks. The outer layer is difficult to demonstrate except at the equatorial margins, and



TEXT-FIG. 9. *a*, *Dictyotidium*, composite of variations included in the author's concept. *b*, *Paleopedicystus* gen. nov. *c*, *Cymatiosphaera*, typical form. *d*, *Duvernaysphaera* gen. nov. *e*, *Multiplicisphaeridium*, composite of variations included in the author's concept. *f*, *M. truncatum* sp. nov., process detail. *g-h*, *M. ramispinosum* sp. nov., process detail. *i*, *M. spicatum* sp. nov., process detail. *j*, *M. ? sprucegrovensis* sp. nov., process detail.

has been lost from most specimens, leaving the broken spine bases as a common characteristic. The shape seems to be lenticular. *Membranilarnax* has branched appendages. *Pterosperma* (*Pterospermopsis*) lacks the spokes, although short stiffening processes, radial thickenings or fluting are developed in some species. The membrane is also larger and heavier in *Pterosperma*.

Duvernaysphaera tennicingulata sp. nov.

Plate 49, figs. 10, 11

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., 5,625' core, Duvernay member. Slide

8, 42.9 120.6; vesicle 32 microns, membrane width 6 microns, rods about 6 microns apart (fig. 10). Illustrated: Imperial Bistcho Lake 7-7, 7-7-124-2W6th M., 4,720' core, Woodbend Group, Slide 5A, 41.2 112.3; vesicle 31 microns.

Diagnosis. Vesicle circular in outline; lenticular; surrounded by a diaphanous flange, both laevigate. Flange stiffened by a number of rods radiating from the vesicle margin, 8–12 microns long, and about 6–9 microns apart. Flange sometimes continued over vesicle surface as a membrane. Compression commonly off-centre. Size 26–33 microns.

Remarks. The membrane is often lost, leaving stubs of the rods to mark its places of attachment.

Genus CYMATIOSPHAERA O. Wetzel

Text-fig. 9c

Type species. *Cymatiosphaera radiata* O. Wetzel 1933.

Description. Spherical, ellipsoidal, or lenticular; often with radial ribs; provided with a membrane that is gathered into polygonal areas on the vesicle surface and that may extend considerably beyond the vesicle margin.

Cymatiosphaera pentaster sp. nov.

Plate 49, fig. 18

Holotype. Imperial Bistcho Lake 7-7, 7-7-124-2W6th M., Beaverhill Lake? equivalent, 4,906–11' core. Slide 1, 28.2 114.9; vesicle 18 microns, 29 microns overall.

Diagnosis. Vesicle circular in outline; surface divided into five equal wedge-shaped areas by ridges originating at the poles and projecting as equatorial projections about 5 microns beyond vesicle equatorial margin, ridges often broadened and somewhat divided beyond the margin; spinose projections and ridges connected by a very thin appressed diaphanous membrane surrounding the vesicle, outer margin of each membrane segment almost straight; always compressed in the equatorial plane, suggesting a lenticular shape; size 28–33 microns overall, vesicle 18–20 microns.

Cymatiosphaera tetraster sp. nov.

Plate 49, fig. 15

Holotype. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Duvernay member, 5,625' core. Slide A, 33.1 113.2; vesicle 20 microns.

Diagnosis. Vesicle circular; shape lenticular; polar areas of both hemispheres bear a diamond-shaped lacuna bounded by a low narrow ridge; from each angle of the lacuna low narrow ridges extend across the vesicle, dividing each hemisphere into four equal segments; ridges extend as spines about 3–4 microns beyond vesicle equator; spinose projections and ridges connected by a thin diaphanous membrane, giving the whole a sub-quadrate shape in polar view; vesicle size 28–34 microns.

Remarks. Polar diamond-shaped lacunae, slightly thicker vesicle wall, and four instead of five rays distinguish this species from *C. pentaster* sp. nov.

Cymatiosphaera perimembrana sp. nov.

Plate 49, figs. 16, 17

Holotype. Imperial Willingdon No. 2, 11-20-55-15W4th M., 2,975–3,050'; picked composited Duvernay cuttings. Slide 1, 36·3 113·2; vesicle 28 microns (fig. 16). Illustrated: same sample, Slide 1, 53·1 114·2; vesicle 24 microns.

Diagnosis. Vesicle spherical to ellipsoidal; laevigate; surrounded by a tightly fitting diaphanous membrane that is gathered into a fine reticulum; lacunae polygonal, 4–8 microns across, muri very fine; membrane stiffened by fine rods that arise from the muri, 3–5 microns long; membrane extends 2·5–5 microns beyond vesicle margin; size range 22–36 microns.

Remarks. The membrane is frequently lost in large part, but remnants of the reticulum remain on the vesicle, and remnants of the muri may be left as spines on the margin. The structure is generally visible only under oil.

Genus *DICTYOTIDIUM* Eisenack 1955 emend.

Text-fig. 9a

Type species. *Dictyotidium dictyotum* (Eisenack) Eisenack 1955.

Description. Vesicle spherical; surface reticulate, ridges low, distinct, lacunar areas polygonal; some species with two distinctly smaller lacunae, one at each pole; small apiculae or spines may arise from the ridges; papillae may be present in the floors of lacunae.

Remarks. The genus is enlarged to include forms with differentiated polar polygons and with short spines or apiculae on the ridges.

Dictyotidium polygonium sp. nov.

Plate 49, fig. 14

Holotype. Calmont Std. Winterburn Prov. No. 1, 10-4-53-25W4th M., Duvernay member, 5,515' core. Slide 2, 47·2 119·3; 29 microns.

Diagnosis. Vesicle circular; surface divided into polygonal areas about 4 microns across with a small raised granule in the centre of each polygon; ridges narrow, rounded, slightly raised above vesicle surface; diameter 27–31 microns.

Dictyotidium polosymmetrium sp. nov.

Plate 49, fig. 13

Holotype. Imperial Bistcho Lake 7-7, 7-7-124-2W6th M., Beaverhill Lake? equivalent, 4,906–11' core. Slide 1, 32 113·3; 21 microns.

Diagnosis. Vesicle spherical; laevigate to faintly roughened (oil); surface divided into large polygonal areas by low narrow ridges; polygons up to 10–12 microns wide; a smaller polygon at each pole with a pore or papilla in its centre, polygon width about 6 microns; size 20–24 microns.

Genus PALEOPEDICYSTUS gen. nov.

Text-fig. 9b

Type species. Paleopedicystus rodeoensis sp. nov.

Diagnosis. Body subspherical, provided with a cylindrical stalk; body thick-walled, spinose, sometimes provided with an enclosing membrane.

Remarks. The superficial resemblance to cysts of some Ochromonadaceae (*Uroglena*) is striking, although no definitely identified members of this group are known from younger Palaeozoic or Mesozoic rocks. The complex structure of the body of *Paleopedicystus* (membrane, complex ornamentation) would seem to exclude hystrichospherids of the type of *Veryhachium clava* Deunff 1959, at least until more species are described and our understanding of the variations of these forms is more complete.

Paleopedicystus rodeoensis sp. nov.

Plate 50, figs. 1-3

Holotype. Bear Rodeo No. 1, 8-20-89-9W4th M., Beaverhill Lake fm., 731-41' core. Slide 1, 30-6 122; overall length 48 microns, body diameter 33 microns, stalk length 21 microns, stalk width at mid-point 8 microns.

Diagnosis. Subspherical body with a cylindrical stalk; body thick-walled with five or more large cone-shaped processes in addition to densely packed irregular verrucose to pilose projections that are most prominent on the hemisphere opposite to the stalk; stalk finely striate at its connexion with the body and twice as broad as the stalk proper, remainder laevigate, pedal extremity constricted without distal opening; much of body covered with a diaphanous indefinite membrane that extends as much as 5 microns beyond the body wall; colour amber-yellow to amber-brown; body wall thickness about 4 microns.

CHITINOZOA

Most specimens of *Lagenochitina* and *Angochitina*, when cleared by chemical means, show a dark interior 'collar' in the neck of the body, convex at its base (Pl. 51, fig. 7). This 'collar' is the remnant of a plug-like cap, shaped much like a bottle stopper, that fits the neck of the body. The plug is spinose in *Angochitina*, the spines generally simpler than those of the body. Specimens of *Angochitina* cf. *devonica* with the plug in place are shown on Plate 51. The plug does not seem as resistant as the body of the chitinozoan. Cysts of certain recent Chrysophyceae (Ochromonadaceae) possess an analogous structure. In *Ochromonas*, the original cyst membrane is of cellulose. The

EXPLANATION OF PLATE 50

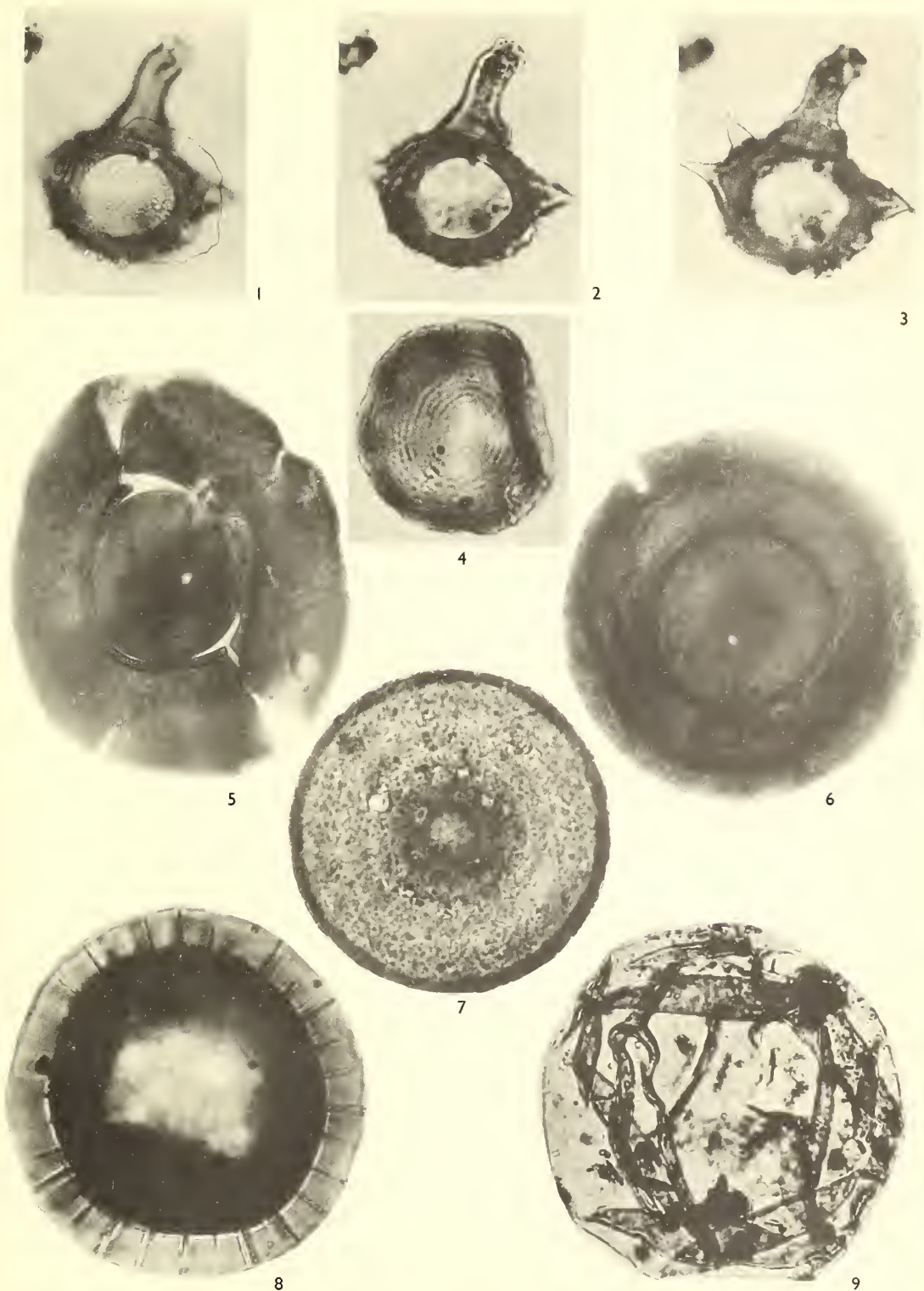
Figs. 1-3, *Paleopedicystus rodeoensis* sp. nov., holotype, high, medium, and low focus respectively. Body diameter 33 microns; stalk length 21 microns.

Fig. 4, *Chomotriletes? bistchoensis* sp. nov., holotype, 49 microns.

Figs. 5-7, *Hoegisphaera glabra* sp. nov. 5, Holotype, 90×141 microns, operculum 57 microns. 6, 123 microns. 7, Operculum 70 microns.

Fig. 8, *Tasmanites* sp. A, 81 microns.

Fig. 9, *Leiosphaeridium fastigatirugosum* sp. nov., holotype, 125 microns.



STAPLIN, Upper Devonian microfossils

outer siliceous coat is formed later by impregnation and is sculptured through the agency of external cytoplasm. The plug as a rule contains little or no silica. In germination the plug is dissolved and the contents of the cyst escape through the pore in the form of motile cells. Pascher (1924) noted that the cyst may be internal or external. If the periplast of the parent is coarse, it remains as an external envelope around the cyst. If the periplast is soft, it is absorbed into the cyst.

Angochitina cf. *devonica* Eisenack

Plate 51, figs. 1-7

1955 *A. devonica* Eisenack, p. 313, pl. 1, figs. 10-12.

1958 Collinson and Scott, pp. 13-15, pl. 1, 3, text-fig. 4.

Figured. Home Grizzly Mt. 10-16, 10-16-69-7W5th M., Beaverhill Lake fm., 7,020-5' core. Slide 1, 36.8 114.5; 110 × 163 microns (fig. 7). Plug, Slide 2, 39.8 110.3, 43 microns, central part 33 microns (fig. 3). Plugged specimen, Slide 2, 39 115.6, plug 42 × 45 microns (fig. 5). Plugged fragment, Slide 2, 32.8 121.8, plug ± 51 microns excluding processes (fig. 4). Wall detail, Slide 3, 43.6 120.6, ± 13-21 microns between spine bases (fig. 6). Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., 5,403' core, Lower Ireton, Slide 5, 34 117, body 93 × 126 microns, plug width 39 microns (figs. 1-2).

Remarks. The length varies from 150 to 210 microns. Spines of the plug and neck are simple, complex at the body mid-point, and simple at the base. The spine branching is dichotomous, with each branch again divided in some cases. The spines are arranged in about eight more or less vertical rows, but the arrangement is obscure on whole specimens. The neck is occupied by a plug that has a bulbous spinose termination above the neck. The small specimen (figs. 1-2) perhaps represents another species.

INCERTAE SEDIS

Genus *HOEGISPHAERA* gen. nov.

Type species. *Hoegisphaera glabra* sp. nov.

Diagnosis. Body spherical. One hemisphere provided with a thickened circular ring, enclosing an operculum. The operculum is often found detached from the body. Colour dark amber-brown. Known species are laevigate to wrinkled.

Remarks. Two additional species are present in the author's collections. One occurs in the type section of the Sylvan shale and the other in the type section of the Tulip Creek formation, both of Ordovician age, Oklahoma. The colour and texture of the wall are similar to those of Chitinozoa, but the analogy cannot be carried farther. The genus is named for Ove A. Høeg, for his contribution to our knowledge of Devonian floras.

Hoegisphaera glabra sp. nov.

Plate 50, figs. 5-7

Holotype. Socony Vegreville No. 1, 14-20-51-15W4th M., 3,500-600', Duvernay decontaminated cuttings. Slide 6, 44.3 110.5; size 90 × 141 microns, width of thickened ring 4 microns, diameter of operculum 57 microns (fig. 5). Illustrated: same sample, Slide 6, 45.3 112; diameter 123 microns, operculum 60 microns. Operculum, Imperial Paddle River No. 1, 5-17-56-8W5th M., 7,823' core, Duvernay-Cooking Lake equivalent, Slide 1, 26.8 116.8; 70 microns.

Diagnosis. Body spherical; laevigate; dark amber-brown. One hemisphere provided

with a thickened circular ring, surrounding an operculum of the same thickness as the body wall. The operculum frequently is detached from the body. Diameter of body 110–130 microns, diameter of operculum 50–58 microns, width of thickened ring, 2–4 microns.

Remarks. The operculum, when etched, shows an indistinct concentric pattern not visible on normal specimens. Both Ordovician species are smaller.

Genus TASMANITES Newton 1875

In his description of *T. punctatus*, Newton remarked on minute lines ('tubes?') passing from the outer to the inner surface. Singh (1932) and this author failed to find these canals in Tasmanite available to them. However, J. M. Schopf (personal communication) and the Jersey Production Laboratory have ample material with the canals. Several species of leiospheres are probably present in the Tasmanite. A detailed discussion of the genus is contained in Schopf, Wilson, and Bentall (1944).

The small species described here has prominent canals that start at the inner wall surface, many not penetrating to the exterior surface. This is the reverse of the situation in *T. punctatus* and species of *Tytthodiscus* seen by the author. Most of the large cysts of the Devonian and Lower Mississippian of Western Canada have thin walls without canals. No 'pyloms' have been noted on North American species of *Tasmanites* (Schopf 1960).

Tasmanites sp. A.

Plate 50, fig. 8

Figured. Imperial Labyrinth Lake 15-14, 15-14-48-23W4th M., Cooking Lake member, 5,730' core. Slide 1, 37.6 121.3; 81 microns, wall thickness 9 microns.

Description. Body spherical; thick-walled; wall punctured with narrow even canals, only part of which reach the outer wall surface, separation about 6 microns; surface laevigate except where canals reach the exterior; colour dark amber-brown.

Remarks. *T. avelinoides* Sommer 1953 (1956) is much larger. The description does not indicate whether all canals reach the outer surface.

Genus CHOMOTRILETES Naumova 1953

Remarks. Naumova published two views of the type species, one face showing a pattern of concentric overlapping arcs, the other two sets of intersecting arcs. The latter could not be demonstrated on the Alberta specimens. No haptotypic structures were noted, although an indistinct trilete was indicated for the Russian specimens. It is not certain that *C. ? bistchoensis* sp. nov. is a plant spore, or that it belongs in *Chomotriletes*.

EXPLANATION OF PLATE 51

Figs. 1–7, *Angochitina* cf. *devonica* Eisenack. 1–2, Plugged individual from lower Ireton member, plug width 39 microns. 3–7, Specimens from Beaverhill Lake fm. 3, Isolated plug, 43 microns. 6, Detail of denuded wall (see text).



STAPLIN, Upper Devonian Chitinozoa

Chomotriletes? bistchoensis sp. nov.

Plate 50, fig. 4

Holotype. Imperial Bistcho Lake 7-7, 7-7-124-2W6th M., 4,159-64' core, Woodbend fm. Slide 1, 21.8 124.5; 49 microns.

Diagnosis. Body circular in outline; surface covered by arc-like ridges that form a concentric pattern, the arcs overlapping, about twelve to sixteen crossed by a radius; ridges less crowded toward the poles, indistinct at the poles; no haptotypic structures noted; size 47-53 microns.

LIST OF WELLS USED IN REEF TREND STUDY

<i>Well</i>	<i>Location</i>	<i>Sampled interval</i>	<i>Map no.</i>
Royalite Texaco—Sharphead No. 1	8-18-44-25W4	6770-6800 ctg.	60
Canadian Superior—Rausch No. 1	12-21-44-27W4	7280-7320 ctg.	69
A. H. C. and E. Camrose No. 1	9-29-46-20W4	5169-5231 c.	10
Royalite Rosecam No. 1	4-14-47-18W4	4470-4560 ctg.	67
Sun Pipestone Creek Province No. 1	5-11-47-24W4	5955-5990 ctg.	65
Amerada Crown CF 42-24	9-24-48-17W4	4085-4170 ctg.	73
Imperial Armena No. 2	3-15-48-21W4	5162-5174 c.	11
Imperial Labyrinth No. 1	15-14-48-23W4	5610 core	29
Millet Leduc No. 16-6	16-6-48-24W4	5971-5986 c.	24
Imperial H. B. Wizard Lake No. 5-26L	5-26-48-27W4	6635-6650 ctg.	22
Imperial Ireton No. 1	4-10-49-26W4	6200-6245 ctg.	53
Anglo-Canadian Beaverhill Lake No. 2	11-11-50-17W4	3837-4038 c.	9
Imperial Tofield No. 1	9-18-50-18W4	4220-4280 ctg.	59
Imperial Joseph Lake West No. 1	15-7-50-22W4	5245-5320 ctg.	77
Imperial Looma No. 1	4-10-50-23W4	5370-5395 ctg.	41
Gas and Oil Offsets Reality No. 1	11-25-50-27W4	5926-5931 c.	23
Socony Vegreville No. 1	14-20-51-15W4	3500-3600 ctg.	57
Redwater Petroleum No. 2	1-29-51-19W4	4390-4435 ctg.	75
Calmont Leduc No. 3	4-14-51-21W4	4840-4895 ctg.	81
C. and S. Shaw No. 1	1-20-51-22W4	5160-5205 ctg.	79
Imperial Foley Lake No. 1	9-16-51-23W4	5265-5285 ctg.	47
Imperial Whitemud No. 1	15-14-51-25W4	5565-5605 ctg.	42
Imperial Graminia No. 2-12	2-12-51-27W4	6120-6170 ctg.	35
Time Texaco Holburn No. 1	4-11-51-1W5	6540-6650 ctg.	37
Texaco Time Brightbank No. 1	4-28-51-2W5	6800-6860 ctg.	33
Imperial Golf No. 1	2-11-52-25W4	5430-5470 ctg.	54
Pan Western West Edmonton No. 1	14-21-52-25W4	5450-5470 ctg.	52
Imperial Golden Spike No. 5	1-27-51-27W4	6005-6060 cores	13
Imperial Redwater Picadilly No. 1	4-17-52-26W4	5975-6005 ctg.	38
Imperial Spruce Grove No. 1	4-25-52-27W4	6065-6120 ctg.	36
Okalta Stony Plain No. 1	5-29-52-27W4	6140-6210 ctg.	39
Imperial Ardrossen No. 1	8-17-53-21W4	4595-4650 ctg.	76
Cal. Std. Winterburn Province No. 1	10-4-53-24W4	5435-5535 core	6

LIST OF WELLS USED IN REEF TREND STUDY (*cont.*)

<i>Well</i>	<i>Location</i>	<i>Sampled interval</i>	<i>Map no.</i>
Texaco (Shaw) Spruce Grove No. 1	4-11-53-27W4	5910-5990 ctg.	40
Scottford No. 1	8-33-54-21W4	4250-4295 ctg.	74
Imperial Riverbend No. 1	4-22-54-23W4	4695-4750 ctg.	55
Imperial Sturgeon No. 2	5-24-54-26W4	5395-5430 ctg.	44
Texaco McColl Onoway No. 1	16-18-54-27W4	6020-6080 ctg.	45
Imperial Duvernay No. 1	6-30-55-11W4	2237-2291 c.	30
Imperial Watt No. 5	5-11-55-14W4	2725-2820 ctg.	66
Imperial Willingdon No. 2	11-20-55-15W4	2975-3050 ctg.	50
Imperial L'Amoureux No. 1	12-8-55-23W4	4750-4820 ctg.	49
Lignora Redwater No. 1	3-1-56-22W4	4145-4180 ctg.	51
Imperial Mearns No. 1	15-6-56-26W4	5435-5525 ctg.	34
Pacific Deadman No. 1	7-32-56-27W4	5460-5590 ctg.	68
Imperial Paddle River No. 1	5-17-56-8W5	7730-7780 c.	4
Texaco McColl Cherhill No. 1	1-34-56-5W5	6590-6640 ctg.	78
Canadian Superior Kozak No. 16-3	16-3-57-17W4	3110-3170 ctg.	64
Imperial Skaro No. 1	15-2-57-20W4	3535-3620 ctg.	62
Imperial Eldorena No. 1	4-27-57-20W4	3577-3589 core	28
Redwater Saltwater Disposal Well	12-28-57-21W4	3628-3632 core	26
Imperial Alcomdale No. 1	14-27-57-26W4	5195-5275 ctg.	63
Royalite Seaboard Delph No. 1	10-17-58-19W4	3350-3410 ctg.	58
Imperial Redwater No. 2	3-29-58-21W4	3780-3315 ctg. } 3850-3885 ctg. }	48
Imperial Opal No. 35	7-29-58-22W4	3830-3910 ctg.	70
Imperial Egremont West No. 6-36	6-36-58-23W4	3835-3905 c. } 3948-4008 c. }	27
Barnsdall Vilna Time No. 1	5-12-59-13W4	2313-2341 c.	12
Imperial Jeffrey No. 1	6-4-59-23W4	4115-4225 ctg.	71
Imperial Westlock No. 14-24	14-24-59-26W4	4890-4925 c.	25
Falcon Seaboard Seminiuk No. 1	2-28-59-19W4	3250-3375 ctg.	72
Great Plains Seaboard Smoky Lake No. 2	14-12-60-18W4	2855-2970 ctg.	82

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NOTE

NORMANICYTHERE LEIODERMA (NORMAN) IN NORTH AMERICA

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THE distribution of *Normanicythere leioderma* (Norman) has been examined in a recent paper (Neale, *Palaeontology* 2, 1959, pp. 72-93) where it was shown to range from Spitsbergen (30° E.) to north-western Greenland (70° W.). Further information regarding its occurrence in North America has recently been obtained which considerably extends its western limits.

Dr. Frances Wagner of the Geological Survey of Canada informs me that she has found this species in a sample dredged from Cabot Strait (47° 30' N., 60° W.) in autumn 1959, and that it is probably represented in two samples from Hudson Strait (61° 30' N., 69° W.). The Cabot Strait specimens consist of one adult male right valve and one complete carapace which appears closest to instar 5. The material from Hudson Strait, which is questionably referred to *N. leioderma*, consists of one female left valve belonging to the penultimate instar dredged from a sandy clay bottom at a depth of 51 fathoms, and a complete female carapace, also belonging to the penultimate instar, obtained from a fine sand bottom at a depth of 145 fathoms. So far Dr. Wagner has not found this species in the Canadian Pleistocene.

Professor F. M. Swain of the University of Minnesota writes that he has found this species in northern Alaska and also believes that it occurs in raised beaches in Lake Champlain, N.Y. The former record extends the range of *N. leioderma* at least another 70 degrees westwards so that it now ranges over more than 170 degrees of longitude. Although it remains to be seen whether any specimens will be forthcoming from the polar seas in the sector covered by the U.S.S.R. it seems probable that the distribution of this species is completely circum-polar, extending southwards to reach an extreme southern limit of approximately 44 degrees of north latitude.

23 March 1960

The University,
Hull

REAPPRAISAL OF THE MESOZOIC MICROSPORE GENUS *AEQUITRIRADITES*

by ISABEL C. COOKSON and MARY E. DETTMANN

ABSTRACT. The Mesozoic form-genus *Aequitriradites* Delcourt and Sprumont is emended with the consequent assignment to it of four species previously referred to the Palaeozoic form-genus *Cirratriradites* Wilson and Coe.

IN 1958 three species of microspores from Australian Lower Cretaceous sediments were referred by us to the Palaeozoic form-genus *Cirratriradites* Wilson and Coe although their close agreement with the Mesozoic form-genus *Aequitriradites* Delcourt and Sprumont was then fully recognized (Cookson and Dettmann 1958, p. 112). Recently, largely as the result of information from M. Delcourt concerning additional examples of the Belgian species *A. inconspicuus* Delcourt and Sprumont, it became evident that this species and the three Australian species referred to *Cirratriradites* all had certain features which are not found in *Cirratriradites*.

The removal of the Australian Mesozoic species from *Cirratriradites* to *Aequitriradites*, thus necessitated, is the main object of the present note. At the same time a broader definition of the genus *Aequitriradites* is proposed and the Russian Cretaceous species *C. interruptus* Bolkhovitina is transferred to *Aequitriradites*. It is apparent from the species now recognized within the genus that *Aequitriradites* has wide distribution, both laterally and vertically, in Mesozoic strata.

Comments. The species *Cirratriradites verrucosus*, *C. tilchaensis*, and *C. spinulosus*, described by Cookson and Dettmann in 1958, are each characterized by a membranous equatorial flange or zona, and by either an opening in or modification of sculpture of the exine at and around the distal pole. This distal opening was considered to have been formed 'by the natural breakdown of the exospore in a circumscribed preformed area' and we still hold 'that as it is a developmental feature neither its presence nor absence can be used for the characterization of individual species' (loc. cit., p. 112). In consequence, specimens with and without a distal opening were referred to each of the three species. Specimens having entire exines (Pl. 52, figs. 3, 4) usually show a distinct, strongly developed sculptural pattern at and around the distal pole. This area of prominent sculpture corresponds in size, shape, and position to the opening in the wall of spores in which a localized breakdown of the distal wall had occurred (Pl. 52, figs. 6, 8, 9, 12). When the opening is not complete both partially and wholly detached sculptural elements can usually be seen about its margin (Pl. 52, figs. 5, 6, 11, 12).

Although the exine opening was not regarded by us as a specific character it was used to determine the generic position of the three Australian species. However, the opening was erroneously regarded as a 'fovea', so that the Australian spores were referred to *Cirratriradites* and not to *Aequitriradites* which differs from the former genus in the absence of foveae. The term 'fovea', as used by Potonié and Kremp (1956, p. 125, fig. 55) in their definition of *Cirratriradites*, refers solely to a sculpture pattern which consists of thinner depressed areas of the exine surrounded by raised, thickened muri

(Schopf, Wilson, and Bentall 1944, p. 42; Potonié 1956, p. 66). The exine in the region of a fovea, although relatively thin, is always entire. On account of the distinction between foveae and distinct exinous openings it is clear that the Australian Mesozoic spores are not conformable with *Cirratriradites*.

That they conform to *Aequitriradites* is evident from their close resemblance to the species of this genus, particularly *A. inconspicuus* which includes spores with a distal exinous opening. The figured type of this species shows such an opening (Delcourt and Sprumont 1955, pl. 2, fig. 6), but originally M. Delcourt considered that this opening was accidental (Cookson and Dettmann 1958, p. 112). Recently, however, M. Delcourt kindly informed us that, after an examination of a large number of specimens of *A. inconspicuus* showing a distal opening, he now regards the opening as a natural exinous breakdown. In order, therefore, to facilitate future identification of spores showing this character we are including a somewhat broader diagnosis of the genus *Aequitriradites*.

SYSTEMATIC SECTION

Infraturma ZONATI Potonié and Kremp 1954

Genus AEQUITRIRADITES (Delcourt and Sprumont) emend.

Diagnosis. Trilete microspores with a membranous zone. Laesurae distinct or only faintly represented especially towards the proximal pole. Exine entire or perforated distally. When perforated, the opening is formed as the result of a natural exinous breakdown about the distal pole. Sculptural elements various.

Distinction. *Aequitriradites* differs from *Cirratriradites* in the absence of foveae and the presence, in some species, of an opening in the distal exine. It is distinct from *Styxisporites* Cookson and Dettmann in the nature of the laesura.

EXPLANATION OF PLATE 52

All photographs are from unretouched negatives. Registered numbers are those of the palaeontological collection of the National Museum of Victoria, Melbourne. Precise locality details are given in Cookson and Dettmann (1958).

Figs. 1, 2, 5. *Aequitriradites verrucosus* (Cookson and Dettmann) comb. nov. P17825, Robe Bore, South Australia, 1,400 ft. 1, 2, $\times 500$, proximal and distal views; 5, $\times 1,250$, showing polar perforation of distal verrucose exine.

Figs. 3, 4. *Aequitriradites verrucosus* (Cookson and Dettmann). P17826, Robe Bore, South Australia, 1,400 ft. Distal views. 3, $\times 500$; 4, $\times 1,250$, showing verrucose sculpture pattern around pole.

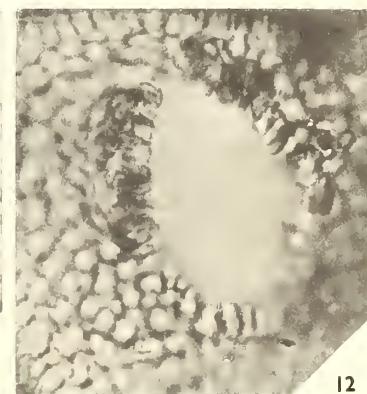
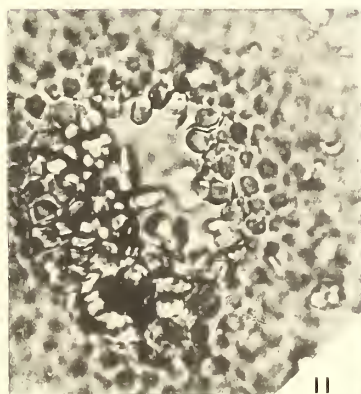
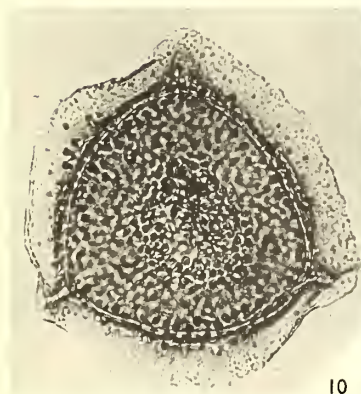
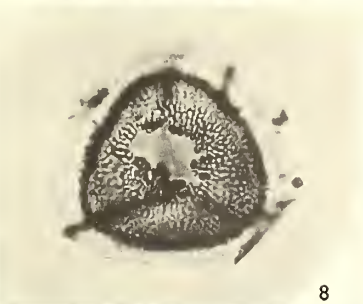
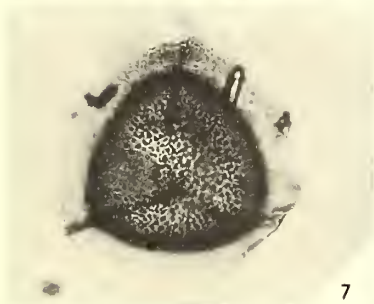
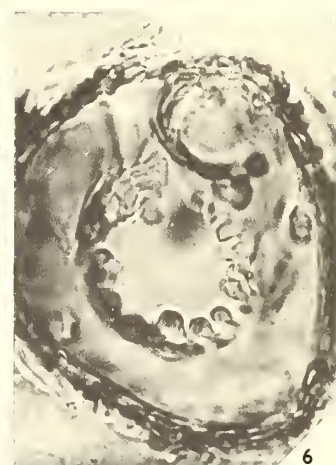
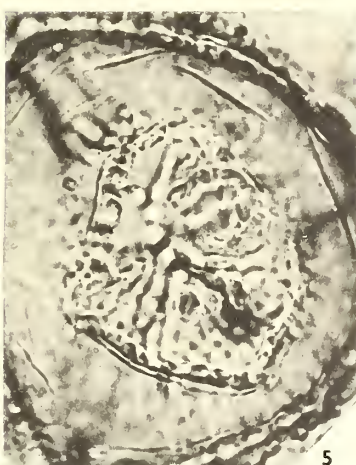
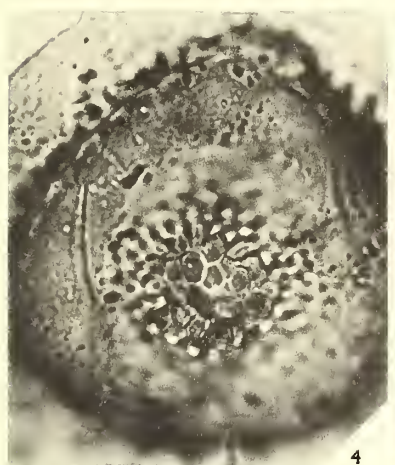
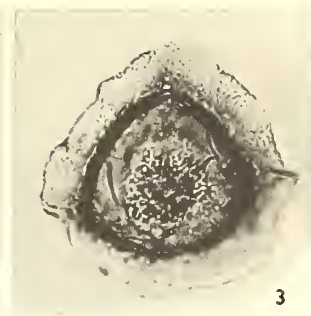
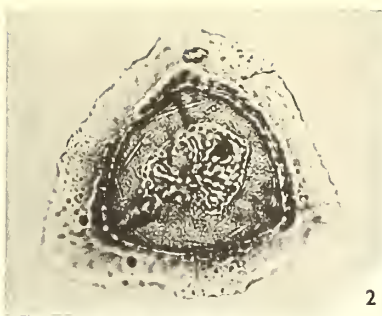
Fig. 6. *Aequitriradites verrucosus* (Cookson and Dettmann). P17827, Robe Bore, South Australia, 1,400 ft., $\times 1,250$. Distal view showing verrucae at margin of polar perforation.

Figs. 7, 8. *Aequitriradites spinulosus* (Cookson and Dettmann) comb. nov. P17828, Gellibrand River (Devil's Kitchen), Victoria. Proximal and distal view $\times 500$.

Fig. 9. *Aequitriradites spinulosus* (Cookson and Dettmann). P17829. Optical section of specimen, $\times 500$, from Gellibrand River (Devil's Kitchen), Victoria.

Figs. 10, 11. *Aequitriradites spinulosus* (Cookson and Dettmann). P17830, Gellibrand River (Devil's Kitchen), Victoria. Distal views. 10, $\times 500$; 11, $\times 1,250$, showing perforated exine and broad-based spinules.

Fig. 12. *Aequitriradites spinulosus* (Cookson and Dettmann). P17818, Gellibrand River (Devil's Kitchen), Victoria. $\times 1,250$, showing regular arrangement of sculptural elements at margin of perforation in distal exine.



Type species. Aequitriradites dubius Delcourt and Sprumont 1955, p. 45; pl. 3, fig. 7. Occurrence: Hainaut, Belgium; Wealden.

Other species. A. inconspicuus Delcourt and Sprumont 1955, p. 45; pl. 2, fig. 6. Occurrence: Hainaut, Belgium; Wealden.

A. salebrosaceus (Maljavikina 1949, p. 65; pl. 13, fig. 14) Nilsson 1958, p. 47; pl. 3, fig. 8. Occurrence: Russia; Lias. Bjuv, Sweden; Rhaetic.

A. sp. A Nilsson 1958, p. 47; pl. 3, fig. 9. Occurrence: Bjuv, Sweden; Rhaetic.

A. verrucosus (Cookson and Dettmann 1958, p. 112; pl. 28, figs. 2–6) comb. nov. Occurrence: eastern Australia; Lower Cretaceous. Viliuisk basin, Russia; Upper Cretaceous (Bolkhovitina 1959).

A. tilchaensis (Cookson and Dettmann 1958, p. 113; pl. 28, figs. 7, 8) comb. nov. Occurrence: eastern Australia; Lower Cretaceous.

A. spinulosus (Cookson and Dettmann 1958, p. 113; pl. 28, figs. 9–13; pl. 29, figs. 1, 2, 5–7) comb. nov. Occurrence: eastern Australia; Lower Cretaceous. Viliuisk basin, Russia; Lower and Upper Cretaceous (Bolkhovitina 1959).

A. interruptus (Bolkhovitina 1959, p. 128; pl. 8, fig. 117) comb. nov. Occurrence: Viliuisk basin, Russia; Lower and Upper Cretaceous.

A. infrapunctatus Lantz 1958a, p. 36; pl. 1, fig. 20, from the Purbeck of L'île d'Oléron, France, subsequently recorded (Lantz 1958b, p. 924; pl. 3, fig. 31) from Purbeck strata of Dorset, England, appears to be a very doubtful representative of *Aequitriradites*. Both specimens figured by Lantz appear to possess a bladder rather than an equatorial zona, suggesting probable conformity with *Zonalapollenites* Pflug.

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CARBONIFEROUS FOSSILS FROM THE KUTTUNG ROCKS OF NEW SOUTH WALES

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ABSTRACT. Brachiopod, polyzoan, molluscan, conulariid, and blastoid faunas from the Booral and Isaacs Formations on the south-eastern side of the Gloucester trough, north of Newcastle, N.S.W., are described. Five new brachiopod genera are established—the spiriferoids *Alispirifer*, *Liriplica*, and *Spinuliplica*; the rhynchonelloid *Lissella*; and the terebratuloid *Booralia*. Twenty new species and one new subspecies are named and described, including the type species of all the new genera. The faunas are not closely related to either the lower Carboniferous or the Permian faunas of eastern Australia, but there are affinities with those of similar age in Argentina. It is concluded that the Booral Formation is Westphalian in age and the Isaacs Formation possibly as late as Stephanian.

INTRODUCTION

THE fossils in the Booral Formation were discovered by Osborne and M'Coy in 1946, and a collection of the bryozoans was described by Crockford (1946). Crockford stated that the fauna came from the Upper Kuttung Series, about 2,000 feet from its top. Osborne (1950, p. 13) confirmed the Upper Kuttung assignment, adding that he considered the fossiliferous strata of the Booral and Limeburner's Creek districts to be 'coeval with freshwater glacial silts and tillites'.

The bryozoans were recognized as being very similar to those of the Neerkol Group of the Rockhampton area and rocks of similar age near Mt. Barney in Queensland. Since most workers at that time agreed in dating the Neerkol Series as Moscovian, the Booral fauna was given a similar age from the commencement of investigations. Hence assuming the accuracy of these correlations, it became possible for the first time to date the early part of the Kuttung glaciation on marine fossil evidence.

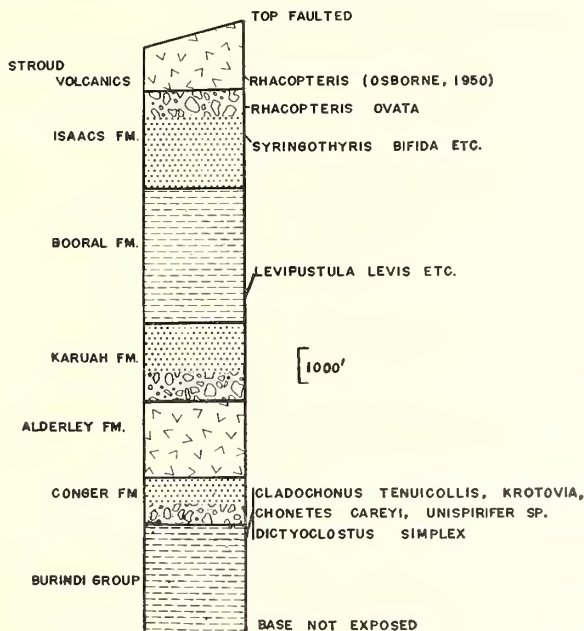
In order to check the position of the fossiliferous horizon in the stratigraphic succession the area has been mapped in more detail than previously, and the results of this work are being published elsewhere. Further fossil localities in the Booral Formation have been discovered, as well as a new marine fossil horizon in the Isaacs Formation, and a plant-bearing horizon in the Karuah Formation. A short paper describing one member of the fauna, the trilobite *Australosutura gardneri* (Mitchell), which also occurs in Argentina, has already been published (Amos, Campbell, and Goldring 1960).

Stratigraphy. Osborne (1950) included the Booral horizon in his Upper Kuttung Series, but he gave no information on detailed correlations. His reason for this dating is the correlation of the thick toscanite unit some 1,700 feet below the fossiliferous beds with the Mt. Gilmore toscanite-dellenite development of the Paterson area, where it marks the top of the Lower Kuttung Series (Osborne 1950, p. 290). There is little doubt that these rocks are all the result of one more or less contemporaneous and very widespread volcanic episode, and there is no reason at the moment to doubt Osborne's correlation.

The upper volcanic rocks of the Booral area (Gloucester Volcanics) were considered (1950, p. 292) to be 'high up in the Glacial Stage', being equivalent to the Paterson Toscanites. This correlation is the result of the equation of volcanic rocks despite their

very different character in the two areas, those at Paterson being exclusively toscanite, while those at Booral are mainly rhyolites and basalts. However, at the present stage no more satisfactory scheme can be offered, and Osborne's suggestion is accepted tentatively.

On this basis, then, the Booral, Isaacs, and Karuah Formations are all equivalents of the Main Clastic Zone of Osborne's Glacial Stage (Osborne 1927), or the Mt. Johnstone Beds of Sussmilch and David (1919). It was in this unit at Glenoak, near Paterson in the Hunter Valley, that Osborne found rocks which he considered to be varves.



TEXT-FIG. 1. Stratigraphic column of the Carboniferous rocks in the Booral area.

It should be noted, however, that no evidence of glaciogene rocks has yet been found in any of these three formations in the Booral-Stroud area, and that the glacial rocks containing marine microfossil debris mentioned by Osborne (1950, p. 25) are not physically continuous with the rocks of this area, the powerful Allworth fault being interposed.

Age and relationships of the faunas. In these faunas there is a total of twenty-three genera. At the present time four of these (*Spinuliplica*, *Liriplica*, *Booralia*, and *Lissella*) are known only from eastern Australia, and three from eastern Australia and Argentine (*Levipustula*, *Alispirifer*, and *Australosutura*). This is a particularly high percentage of 'Gondwana' types, especially when it is considered that the remaining sixteen genera include the broadly conceived *Rhombopora*, *Fenestella*, *Polypora*, and *Sanguinolites*.

In relation to the Lower Carboniferous faunas of the continent, these faunas present a revolutionary aspect. Only nine genera are known to be held in common, *Phricodothyris*, *Alispirifer*, *Syringothyris*, *Fenestella*, *Polypora*, *Fistulammina*, *Sanguinolites*, *Posidonia*, and *Cypricardinia*. The number of genera persisting through to the Permian in the

area is unknown, but it is unlikely to be more than eight. Included in these are *Fenestella*, *Polypora*, *Composita*, *Sanguinolites*, and *Limipecten*.

The age of the fauna is difficult to determine. The *Levipustula* faunas are well known in Queensland where they overlie coralline limestones dated as Upper Viséan (Hill 1934), by an interval of approximately 1,000 feet (W. Fleming, pers. comm.). Whitehouse (unpubl.) and Maxwell (1951) have both considered the Neerkol Group in which *Levipustula* occurs to be of Moscovian age, the main evidence being the similarity

TABLE I

Section of Fossiliferous Rocks east of Booral

The fossiliferous unit varies considerably in thickness along the strike, and the section below has been taken through its thickest part, near 019840. Only the most prominent fossils in each unit are listed.

TOP

1. Barren Sandstone.
2. Band of crinoidal siltstone containing *Liriplica alta* and *Booralia ovata*. Thickness 2 feet.
3. Dense black siltstone with abundant crinoid columnals and containing richly fossiliferous lenses with *Alispirifer lamellosus*, *Spinulicosta spinulosa*, *Levipustula levis*, *Fistulamina frondescens*, *Fenestella* spp., and *Polypora* spp. Thickness 30 feet.
4. Dense black mudstones, in places silicified, but with few fossils. Thickness 50 feet.
5. Mudstone crowded with *Levipustula levis*. Thickness 10 feet +.
6. Grey to black mudstone with abundant smaller fossils including *Spinuliplica spinulosa*, *Lissella booralensis*, *Composita magnicarina*, *Fistulamina frondescens*, *Fenestella* spp., and *Polypora* spp. Thickness 30 feet.
7. Hard, grey to black siltstone, with quantities of comminuted carbonaceous material, and containing *Alispirifer lamellosus*, *Spinuliplica spinulosa*, *Phricodothyris booralensis*, *Composita magnicarina*, *Levipustula levis*, *Fistulamina frondescens*, *Fenestella* spp., *Limipecten flexiauriculus*, and *Calloconularia minima*. Thickness 25 feet.
8. Black mudstones with *Fistulamina frondescens* and crinoid columnals. Thickness 10 feet.
9. Barren coarse sandy beds.

between the associated *Spiriferellina neerkolensis* and *Neospirifer pristinus* and certain American Pennsylvanian species.

Outside Australia *Levipustula* is known from the Westphalian B and basal Westphalian C of the Franco-Belgian coalfield and Britain, and from an unknown horizon in the Karaulakh Mts. of Russia, as mentioned by Maxwell (1951). Our species are most similar to *Pustula rimberti* Waterlot, of the lower Westphalian C.

Although the genus *Limipecten* is known from Viséan rocks in Britain, it does not become abundant or widespread throughout the world until middle Westphalian times, as for example in the Des Moines Series of North America. At least three species of this genus are known to be associated with the *Levipustula* faunas in New South Wales, suggesting that they are not older than Middle Westphalian.

Lissochonetes has not yet been found in the Booral Formation, but farther east at Bombah Point on the Myall Lakes it is found with an *Alispirifer-Levipustula* fauna. This genus is not known anywhere in the world earlier than the base of the Pennsylvanian.

Alispirifer has been found by Mr. B. A. Engel (pers. comm.) in association with *Marginirugus* on horizons much lower than the Booral Formation, and probably as low as the early Viséan. However, in Argentina, Amos (1958) has recorded two species of

'*Spirifer*', which probably belong to *Alispirifer*, from the upper part of the Tepuel System, the tentative age of which he considers to be Moscovian.

Information available at the present time is that *Calloconularia* is restricted to rocks of Pennsylvanian age, and though the data are admittedly incomplete, it remains as some support for a post-Viséan age for the Booral fauna.

The occurrence of *Syringothyris* in the Isaacs Formation may be construed as evidence in favour of an earlier age in the same way as Harrington (1938) used *S. keideli* as an indication of a Lower Carboniferous age for the San Juan tillites of Argentina. However, syrinx-bearing syringothyrinoids are known to occur as high as the Agglomeratic Slate in Kashmir (*S. lydekkeri*), and Amos (1958) has found a species related to *S. keideli* in the Upper Tepuel System (see above).

Both developments of marine fossils lie beneath beds containing a rich *Rhacopteris* flora. In the past, so far as Australian geologists have been concerned, this genus has been considered to be a Lower Carboniferous index (Walkom 1944). However, in South America it is known to range up into the Itararé Group of Pennsylvanian age, where it is associated with rocks of glacial origin (Caster 1952). Under similar climatic conditions there seems to be no reason why it should not have a similar range in Australia.

All the positive evidence supports an age not older than Pennsylvanian for the Booral fauna, while the evidence of *Levipustula* and *Limipecten* favours Middle Westphalian. The negative evidence, e.g. the absence of any distinctive lower Carboniferous genera, also favours this interpretation. The fauna of the Isaacs Formation is possibly as young as the Stephanian.

SYSTEMATIC DESCRIPTIONS

Order CONULARIIDA Miller and Gurley 1896
 Suborder CONULARIINA Miller and Gurley 1896
 Family CONULARIIDAE Walcott 1886
 Subfamily PARACONULARIINAE Sinclair 1952
 Genus CALLOCONULARIA Sinclair 1952

Type species *Calloconularia strimplei* Sinclair, Upper Pennsylvanian of Oklahoma.

Remarks. See Moore and Harrington (1956, p. 65).

Calloconularia minima sp. nov.

Holotype. F.4123A; paratypes F.4123B–G; from the Booral Formation below the main *Levipustula* bed, near 019840.

Description. Faces of equal width; unknown whether transverse section square or rhombic; apical angle ranges from 20° to 26°; corners with well-formed furrows; shell somewhat thickened in corners; transverse ribs narrow, rather closely spaced, and much narrower than interspaces; measurements of number of ribs on mid-face of three specimens at given distances from the apex are:

	<i>Specimen 1</i>			<i>Specimen 2</i>	<i>Specimen 3</i>		
Distance from apex in mm.	15	25	35	c. 45	10	15	20
Number of ribs per 3 mm.	9	6	5	3	12	10	7

transverse ribs slightly deflected adorally in corner angles, and those of adjacent faces

alternate; on mid-face a distinct ridge across which ribs show an even curvature, or more frequently sub-angular flexure; ribs both continuous and alternate, sometimes showing both conditions on one face; very fine cross-bars, often not visible on adapical portions of test, between ribs; they number about five per mm. at a distance of *c.* 30 mm. from apex; internal moulds also with extremely fine cross-bars at same spacing; at adoral end of internal moulds, crests of infillings of transverse ribs show very fine shallow incisions, indicating thickening of test in this position; apex and aperture not observed.

Remarks. I am in doubt as to whether this species should be referred to as *Paraconularia* or *Calloconularia*. Moore and Harrington (p. 65) give as a generic character of *Paraconularia* 'mid-line on faces indicated only by slight deflection of ribs along it'. In my specimens there is a distinct ridge along the mid-faces, and hence they would appear to be excluded from that genus. Despite the above statement, however, the figures of *Paraconularia* given by these authors include many in which the mid-line is marked by alternating transverse ribs. No details of the mid-face of *Calloconularia* are given.

Class BLASTOIDEA

Genus PENTREMITES Say 1820

? *Pentremites* sp.

Plate 56, fig. 2

Material. F.4714c, from the beds below the main *Levipustula* bed, near 019840.

Description. A single radial plate, length about three times width; ambulacral area *c.* 0.5 of total plate length, narrow, and with narrow, sharp, everted margins; triangular area below ambulacrum separated off from remainder of plate by its slightly greater arching, and by the abrupt change in direction of growth lines at its margins; profile of basal edge almost straight; upper edges not observed; ornament of growth-lines only.

Remarks. The upper part of this plate is badly broken and so the proportions given above are only estimates. The contour and outline indicate that the basals also must have been elongate and hence that the vault/pelvis ratio was low—probably slightly less than 0.5—and that the pelvic angle was correspondingly low. The form of the whole calyx must have been similar to that of the more elongate representatives of *Pentremites okawensis* Weller.

Its Carboniferous age together with the morphological data suggest that the specimen could be placed in any one of the genera *Pentremites* Say, *Orophocrinus* von Seebach, or *Metablastus* Etheridge and Carpenter.

Suborder PRODUCTOIDEA Maillieux 1940

Superfamily PRODUCTACEA Waagen 1883

Family OVERTONIIDAE Muir-Wood and Cooper 1960

Subfamily OVERTONIINAE Muir-Wood and Cooper 1960

Genus LEVIPUSTULA Maxwell 1951

Type species *L. levis* Maxwell, Neerkol series of Queensland.

Diagnosis. See Muir-Wood and Cooper 1960.

Remarks. The spine bases do not appear to be divisible into the three groups as suggested by the above authors. There is no independent row along the hinge, but there are several rows set obliquely to the hinge in many specimens. On others the auricular spines are irregularly arranged. The arrangement of the spines on the body of the pedicle valve is irregular to quincuncial. There are also fine spines on the brachial valve.

There is a close comparison between *Levipustula* and the forms referred by Waterlot (1932) to *Productus* (*Pustula*) *piscariae* and *P. (P.) rimberti* from the Westphalian of northern France. One possible point of distinction is a slight sinus in some specimens of *P. rimberti* but this is not a constant character, and in fact may be due to slight distortion of the specimens. Demanet (1943) referred Belgian Westphalian forms to both of the above species, and these show the long upright spines on the ears, the trifid dorsal face of the cardinal process, and the non-dendritic adductor muscle scars in the brachial valve (Demanet pers. comm.). Whereas Waterlot records that in his specimens of *P. rimberti* the spines are developed from the middle of the spine bases, Demanet informs me that in his specimens they are given off from the anterior extremity as they usually are in *Levipustula*. Both the French species occur in Britain and I have examined numerous specimens in the Geological Survey and Museum.

Levipustula levis Maxwell

Plate 56, figs. 18–30

1951 *Levipustula levis* Maxwell, p. 11, pl. 2, figs. 4–13.

Material. Many hundreds of specimens from all levels in the fossiliferous part of the Booral Formation.

Remarks. Specimens from both mudstone and sandstone are available and show some differences, chiefly in the density of the spines. The following comments are intended only as a supplement to already published descriptions.

Body of pedicle valve ornamented with very fine concentric growth-lines together with occasional minor rugae; spine arrangement varies from quincuncial to irregular; decrease in spine density on trail common; occasional specimens with irregular bands of spines on trail, or with very elongate spine bases; on body of valve spines invariably developed from front end of spine bases, which vary greatly in length even over small areas of shell, adjacent individuals on one specimen are 2 mm. and 6 mm.; average length of bases 3 mm.; auricular spines on circular bases, stand out at high angle to shell, and often arranged in a roughly linear pattern of three to five rows directed antero-laterally from the hinge at angles of 10°–20°; occasionally irregularly arranged; size of auricular spines increases away from umbo.

Brachial valve with gently concave visceral disk and narrow geniculate margins; umbo very small (c. 0.5 mm.) and convex; ornament of short oval depressions and fine spines; depressions very variably developed in size and number, and may occur over whole valve or be restricted to anterior and lateral portions; spines much finer than those of pedicle valve, usually absent within 5 mm. of umbo, and less frequent on trail than body of valve; spines arise directly from shell or from very short bases, and directed at a high angle to the shell surface.

Pedicle interior often with a thickening just forward of the hinge and running inside the flanks.

Ventral surface of cardinal process either gently rounded or with a shallow medium

groove; ventral tip of process slightly bifid, and its dorsal surface deeply trilobed, the central lobe in some specimens bearing a very fine shallow depression; cardinal ridges strong and usually terminate before reaching cardinal extremities, but occasionally continue down the lateral margins for 5–10 mm.; adductor scars on subtriangular platforms which usually extend beyond anterior edge of scars themselves; brachial ridges rarely seen, but arise from antero-lateral edge of muscle platform, run antero-laterally and then swing round in a broad loop with the distal tip deflected in towards the septum.

Suborder SPIRIFEROIDEA Allan 1940

Superfamily SPIRIFERACEA Waagen 1883

Family SPIRIFERIDAE King 1846

Subfamily ACROSPIRIFERINAE Termier and Termier 1949

Genus ALISPIRIFER gen. nov.

Type species *A. laminosus* sp. nov., Booral Formation.

Diagnosis. Alate spiriferoids; hinge-line less than maximum shell width at early growth stages but becoming mucronate in adolescence and adulthood; pedicle cardinal area of moderate height, concave, with blunt terminations, and bearing numerous denticle grooves; sinus simple except for a very weak median plication which is not invariably developed; lateral slopes usually with eight to twelve simple rounded plicae, but very occasionally a plica bifurcates; the most lateral plicae very weak and often slightly sinuous; surface of both valves crossed by closely spaced regular concentric growth-lines and irregular growth halts, and by very fine radial lirae; lirae number about fifteen per mm., and are in line on adjacent lamellae; umbonal cavities of pedicle valve obliterated by shell thickening; dental lamellae almost completely involved in the thickening; distinctively rounded callus between the posterior edges of the dental lamellae and obstructing the posterior half of the delthyrium; small callus immediately beneath the brachial umbo carries the platy cardinal process; sockets small; brachial myophragm very weak where it joins the umbonal callus, but may thicken between the central pair of adductors; postero-lateral pair of adductor scars on the furrows bordering the fold and extending back to the umbonal callus.

Remarks. Two other genera are closely comparable with *Alispirifer*—the Devonian *Acrospirifer* Wedekind and the Permian *Pterospirifer* Dunbar.

In Greenland specimens of *Pterospirifer* the delthyrium is 'overarched by a high delthyrial covering that looks like a deltidium. Its surface sculpture is not sufficiently well preserved in the specimens seen to indicate it is a true deltidium or a symphytium' (Dunbar 1955). King (1850) described an English specimen referred to the type species, in which the delthyrium is almost completely arched over by a single strongly lamellose plate. I have been able to confirm this on several Magnesian Limestone specimens in the Sedgwick Museum and in the Geological Survey and Museum. Nothing comparable occurs in *Alispirifer*.

In the German *Pterospirifer alatus* there are sixteen to twenty plicae on each side of the sinus (Malzahn 1937, p. 38). On the Greenland specimens, Dunbar records the presence of 'a dozen or more rounded plications . . .', and in the British specimens there are twelve to sixteen. Bifurcation is a fairly frequent phenomenon. In *Alispirifer* there are fewer

than a dozen plicae, and bifurcation is rare. The sinus in *Pterospirifer* from all localities is from three to five times the width of the bordering plicae. In *Alispirifer* the sinus is relatively much narrower.

The internal structures of *P. alatus* are not well known. Dunbar records that the posterior part of the pedicle valve is 'considerably thickened by later shell growth', but no figures are given. The English specimens also are thickened across the shoulders but the extent of the thickening is not comparable with that of *Alispirifer*, in which the delthyrial cavity forms a pronounced finger-like extension. The brachial valves of these specimens show the presence of 'septa' supporting the crural plates, but such structures do not occur in *Alispirifer*.

Acrospirifer is of Lower and Middle Devonian age, and I can find no record of it in Upper Devonian or Lower Carboniferous rocks. At the present stage of our palaeontological knowledge, however, it would not be safe to place much weight on this apparent temporal discontinuity. The morphological similarities between the two genera are striking, and the differences slight. The chief points of distinction are: (1) There is no delthyrial callus in *Acrospirifer*. (2) The brachial myophragm of *Acrospirifer* develops as a rather broad triangular structure from the thickening in the notothyrial cavity, whereas in *Alispirifer*, although it is sometimes in contact with the notothyrial callus, it does not derive from that structure, and its posterior extremity is invariably fine and low. (3) There appears to be some doubt as to the structure of the radial ornament of *Acrospirifer*. Mailleux (1936) has described specimens of the type species, *A. primaevus* (Steininger) in which there are fine radial lirae which do not appear to be interrupted by the concentric 'striae'. These observations have been confirmed for the same specimens by Allan (1947, p. 448). Solle (1953, p. 29) in his diagnosis of the genus makes no mention of radial lirae, but speaks only of growth laminae and papillae arranged in rows. Fine surface sculpture may therefore prove to be a point of distinction from *Alispirifer*. (4) The delthyrium in *Acrospirifer* is partly covered by a simple, highly arched plate. (5) The notothyrial cavity in *Acrospirifer* is usually only slightly thickened, and the cardinal process is not on a large boss.

Alispirifer is widespread in the post-Lower Burindi rocks of New South Wales, and is represented by several species. It probably occurs in Argentine also.

Alispirifer laminosus sp. nov.

Plate 55, figs. 17-23

Holotype. F.4938; paratypes F.4940-F.4945 from beds above and below the main *Levipustula* bed, near 019841.

Description. Shell very transverse and the extremities almost invariably mucronate; in most specimens mucronation slight, but in others long slender mucros developed, the largest (relatively) observed being about 10 mm. long on a specimen 75 mm. in total width; cardinal area proportionately wide and only slightly concave, except immediately beneath the umbo, where the concavity is greatly increased; cardinal ridges very angular; considered as a whole, area slightly apsacline—almost orthocline; well-developed slightly irregular denticle grooves over entire surface of cardinal area; cardinal area tapers towards the cardinal extremities, where it is abruptly terminated; margins of delthyrium clearly defined by narrow dental ridges; delthyrial angle averages 50°-55°;

sinus narrow (sinal angle averages 23°), and either simple or bearing faint median elevation or flattening, scarcely prominent enough to warrant the term plication; lateral slopes simply plicate, no plication observed to bifurcate and no intercalation; nine to twelve rounded plicae on each side of the sinus in adults, the most lateral ones tending to become quite irregular; plicae approximately of same size as interspaces, the latter being slightly more angular than the former; whole surface (excluding the cardinal area) covered by regular closely set growth lines, and irregularly spaced lamellae which tend to become more regular towards the front of the shell; very fine radial lirae (about 15 per mm.) cover the surface; lirae appear to be in line on adjacent lamellae, and occasionally run continuously across successive lamellae, causing slight serration in their edges.

Brachial valve much less convex than the pedicle; cardinal area well developed, slightly concave, almost parallel sided, and anacline; median fold narrow, rounded on top or gently flattened.

Umbonal cavities of pedicle valve almost entirely filled with callus; postero-dorsal part of the delthyrial cavity occupied by a callus with a rounded dorsal surface which usually projects very slightly through the delthyrium beyond the plane of the cardinal area; margins of delthyrium not obscured by this callus since its edges unite with the inner faces of the dental lamellae on the inner side of the edges of the delthyrium; posterior half of the delthyrium usually obstructed by callus; muscle field in adults almost as wide as long, but in juveniles relatively narrower; muscle field folded by the plicae which border sinus; second lateral pair of plicae sometimes visible on outer edges of field, but always much reduced; adductor scars indefinite and very variable in outline; diductors scars usually longitudinally striated; genital pits distributed across the shoulders for half the width of the shell and for 4 or 5 mm. forward of the muscle field.

Cardinal process on face of well-developed callus situated between sockets; sockets themselves unusually small for a shell of this size, but socket plates quite thick; crural plates small, do not reach to the floor, and not supported on adminicula; posterior end of adductor scars project into small cavity dorsal to umbonal callus; in adults posterior edge of the central pair of muscle scars approximately 5 mm. forward of the edge of umbonal callus; length of central scars *c.* 8 mm.; lateral scars occupy the plication bordering the fold, but may extend sideways on to first lateral plica near their rear extremity; myophragm touches the callus, increases slightly in size between the central adductors, and dies out at their anterior extremity.

Remarks. The denticle grooves on the cardinal area of the pedicle valve vary very considerably in depth. Since all the specimens are preserved as moulds, it is possible that differential solution of the denticle traces took place before the consolidation of the enclosing sediment (Young 1884), and that the varying depth of the grooves is the result of differing degrees of solution.

In most specimens the adductor scars of the pedicle valve are situated in a shallow furrow and extend the whole length of the muscle field. In others they are restricted to the anterior two-thirds of the field. In outline they vary from parallel sided to canoe shaped. The myophragm varies from a small notch at their posterior edge, to a fine ridge extending over almost their entire length.

Both '*Spirifer*' *chubutensis* and '*Spirifer*' *sp.*, which Amos (1958) has described from the upper part of the Tepuel System of Argentina, are to be referred to this genus, but the preservation of the material is too poor to warrant specific comparison.

The species is common throughout the Booral Formation and occurs on all levels.

Alispirifer laminosus undatus subsp. nov.

Plate 63, figs. 3–4

Holotype. F.4765; *paratypes* F.4756–F.4764, Isaacs Formation near 987823.

Description. This subspecies differs from the parent species in the irregular, wavy form of many of its plicae, and in the bifurcation of occasional plicae. Neither of these features is present on all specimens, nor even on most. Also, the callus within the delthyrium of *A. laminosus* is usually much stronger than in *A. l. undatus*, and the denticle grooves on the cardinal area of its pedicle valve are slightly more widely spaced and more irregular.

Remarks. This subspecies is distinguishable only on a population basis, as there is a considerable overlap in all features with the parent species.

Subfamily PHRICODOTHYRINAE Caster 1939

Genus PHRICODOTHYRIS George 1932

Remarks. This genus was reviewed by me in 1955. Since that date two new species have been described from New South Wales by Cvancara, and there is other additional information from specimens from several new localities and horizons.

The spines of *P. immensa* each consist of a pair of incomplete tubes, a split being present along the edge facing the shell. Though no actual spines of other species have been observed, the structure of the spine bases (Cvancara 1958, pl. 111, figs. 25–26) clearly suggests that they also were split in the same way. George (1932, p. 528) figures the spines of *Phricodothyris* as complete tubes, and the spine bases as completely enclosed.

None of the N.S.W. species has small pustules between and in front of the spine bases as do *P. monopustulosa* Demanet and *P. tripustulosa* Demanet, and some undescribed British species.

No transverse barbs have been observed on the few spines of *P. immensa* available.

George (p. 527) comments that 'the development of spines (in *Phricodothyris*) on successive lamellae is not, other than exceptionally, in radial linear series'. On most of our species the arrangement of the spines is frequently, though not invariably, radial. Both radial and non-radial sectors sometimes occur on the one shell.

These features, coupled with the invariable development of strong dental lamellae, ventral adminicula, and median septa, may yet require the removal of the New South Wales species from *Phricodothyris* and their inclusion in *Kitakamithyris*. However, more details of the spines of *Kitakamithyris*, and of the occurrence of double-barrelled spines on species with a '*Reticularia*'-like shell form in western Europe, are required before definite conclusions can be reached.

The internal radial ornament common to the whole group of reticulate spiriferids has never been described in detail, and its function remains unknown. Several features which need explanation have been observed in our specimens. Increase in the number of radial

ribs takes place both by bifurcation and implantation. Some ribs are very short and imper-sistent. Others after bifurcating reunite. On the pedicle valve, at least, ribs are present on the inner surface of the palintrope. On well-preserved specimens ribs are never developed around the margins. It is fairly certain, therefore, that they are not deposited at the mantle edge but are the result of later deposition by the inner surface of the mantle. They are not obliterated on the older parts of the shell by the filling up of the intervening furrows, but they are almost always partly preserved on the muscle fields.

hey can scarcely be related to the pallial system because of their general disposition and their presence inside the palintrope where no pallial sinuses are present. They cannot be related to the presence of strong mantle setae (i.e. setal tracks) because they are not mantle edge phenomena, and obviously there can be no setae along the hinge. Their origin remains obscure.

Phricodothyris booralensis Campbell

Plate 54, figs. 1-3

1955 *Phricodothyris booralensis* Campbell, p. 381, pl. 18, figs. 18, 19.

Neotype. F.4903A from the Booral Formation near 019840.

Remarks. The types of this species were destroyed in a fire at the University of New England in February 1958. The above neotype has been selected from several topotypes which have since come to hand. From these specimens it has been possible to add the following details to the original description.

Pedicle umbo prominent (not small as previously thought probable); cardinal area high, and bearing shallow denticle grooves numbering five to seven per mm.; dental ridges prominent; hinge line about four-fifths of the maximum shell width; ventral adminicula slightly divergent to subparallel along the floor of the valve, and extending approximately one-quarter of its length; dental lamellae strong; median septum reaches maximum height (between 1 and 2 mm.) near its posterior extremity and maintains it over almost its entire length; in transverse section median septum usually broad at base and with a much narrower capping lamella, but some specimens show a simply triangular section; on the inner face of each dental lamella are a pair of low ridges increasing in strength towards the umbo; external pair unite on the umbo, and internal pair coalesce to form a pronounced flange restricting the apex of the delthyrium.

Crural plates large, thick, strongly concave on their inner (notothyrial) faces, and fusing with the floor of the valve for a short distance in front of the cardinal process leaving small umbonal cavities; socket plates thick; sockets very small; cardinal process concave, formed of up to about forty plates in available specimens; thick smooth callus forward of cardinal process produced into a gradually diminishing myophragm; adductor scars large and ovoid, but poorly defined.

Fine radial ribbing on interior of both valves, ribs numbering two to three per mm.

Phricodothyris immensa sp. nov.

Plate 54, figs. 4-11, and Plate 59, fig. 5

Holotype. F.4917C; paratypes F.4914G, F.4915A-D, F.4916B, F.4917B, F.4918-F.4919, from the Isaacs Formation at 987823.

Description. Shell very large for genus; hinge-line only slightly shorter than maximum width of shell, and cardinal extremities subangular to rounded; pedicle valve more strongly convex than brachial, particularly in umbonal regions; pedicle umbo high and moderately incurved over a concave cardinal area; fine irregular ridges, many of which bifurcate towards cardinal ridges, on pedicle cardinal area; eight to ten ridges per 5 mm. along the hinge; no hinge denticles observed; delthyrium wide and open (delthyrial angle c. 45°); no delthyrial covering plates present; narrow (sinal angle $18-25^{\circ}$), shallow, median sinus extends from umbo; concentric ornament regular, with lamellae spaced eight to ten per 10 mm. medially; this spacing uniform at all except final adult stages, where crowding always occurs; lamellae quite distinct but frequently not very sharply defined; eight to eleven spine bases per 5 mm. medially, at all growth stages; spine bases all clearly divided into two, the bifid portion usually occupying slightly more than half the length of each lamella; pointed posterior portion of scar, so common in members of this group, very rarely visible, and where present is on posterior half of lamella; no pustules between major spine bases.

Brachial valve more or less oval in outline; low rounded fold extending from umbo, and bordered on either side by narrow and slightly flattened strips; commissure unipligate; specimens with cardinal area 5 mm. high common; notothyrium very broad, (notothyrial angle $80-90^{\circ}$); cardinal area ridged after same fashion as that of pedicle valve.

Dental lamellae strong and supported on thick adminicula; thickening of dental lamellae, particularly on their outer faces, common, and their inner faces often bear one or two strong longitudinal ridges; adminicula run either a straight course along floor of valve, or are slightly concave toward each other; angle of divergence along floor of valve is about 25° ; from their anterior ends run very low rounded ridges which converge towards the mid-point of the valve, and bound the canoe-shaped muscle field; in the apex of delthyrial cavity is a small callus from which develops a median septum of variable height (2 mm. maximum) extending whole length of muscle field; adductor and diductor scars indistinguishable; inside upper half of delthyrium is a narrow thickened plate arching over beneath the umbo, and formed from two thickened ridges on inner faces of dental lamellae; in occasional specimens this plate united with median septum for a short distance; whole of inner surface covered with radial ornament typical of reticulate spiriferids, but unusually coarse and deep, there being six to ten ridges per 5 mm. on median portion of lateral slopes; size of these ridges diminished on muscle field, particularly around its margins.

Crural plates long and deep, and concave on their inner faces; crural plates welded to floor of valve for a short distance, but never supported by adminicula; at apex of slightly thickened region between bases of crural plates is large striated cardinal process, formed of from twenty-five to forty-five separate plates, median one of which often slightly larger than others; from edge of sessile portions of crural plates arise low rounded ridges which diverge slightly forwards and then arch around to meet at a point one-half to two-thirds of the length of the valve, thus isolating a very large, ovate muscle field; not possible to differentiate two pairs of adductors except at the posterior margins, where short thickened projections from umbonal thickening divide off the central pair; very low myophragm runs length of field; sockets straight, not enclosed at apex, and socket plates not thickened; descending lamellae and spires robust; individuals of moderate size with about twenty volutions in spire.

Remarks. This species is obviously related to *P. booralensis* and at first the two were considered to be conspecific. However, *P. immensa* sp. nov. has (1) much coarser internal radial ornament—six to ten ridges per 5 mm. as opposed to ten to fifteen in *P. booralensis*; (2) coarser ornament on the cardinal areas of both valves; (3) broader muscle fields in both valves; (4) a stronger umbonal thickening in the brachial valve; (5) a more deeply impressed anterior part of the pedicle muscle fields; (6) heavier crural plates.

Superfamily PUNCTOSPIRACEA Cooper 1944

Family SPIRIFERINIDAE Davidson 1884

Subfamily SPIRIFERELLININAE Paeckelmann 1931

Genus LIRIPLICA gen. nov.

Type species *Liriplica alta* sp. nov., Booral Formation.

Diagnosis. Shells of medium size; both valves rather strongly convex; pedicle umbo high and incurved; lateral slopes curve around on to distinct but obtuse cardinal ridges; hinge-line less than maximum width of shell and cardinal extremities rounded at all growth stages; approximately six low, rounded, plicae on each lateral slope; median sinus two to three times wider than the bordering plicae, and carrying a low, rounded, median plica; fold distinct and bearing a median furrow on its anterior half; surface of both valves crossed by fine regular growth-lines and coarse irregularly spaced growth halts, and by very fine discontinuous radial lirae; umbonal cavities of pedicle valve obliterated by massive shell thickening which extends as far forward as the edges of the dental lamellae; strong callus in apex of delthyrium buttressed to inner faces of dental



TEXT-FIG. 2. Diagrammatic sections across two spines of *Phricodothyris immensa* sp. nov. Reconstructed from moulds, F.4939A-B. $\times 75$.

lamellae by thickened outgrowths; strong median septum; brachial valve thickened along hinge; crural plates curved inwards and meeting immediately beneath the umbo to support the flat, platy, cardinal process; central adductor scars restricted to crest and sides of the median fold; postero-lateral scars on bordering furrows and may encroach posteriorly on to the first lateral plicae; spires and jugum unknown; punctae irregularly arranged and numbering about ten to fifteen per sq. mm.; diameter of punctae in inner shell layer 0.015 to 0.04 mm.

Remarks. This genus is similar externally to Reed's poorly known genus *Paraspiriferina*. The following points suggest that the two are distinct: the absence of a plica in the sinus of *Paraspiriferina*; the fact that Reed mentions nothing about fine surface ornament, apart from lamellation, when we know from his other descriptions that he was fully aware of the importance of such; and the fact that the records of similar Permian forms elsewhere in the world (e.g. *Spiriferina multiplicata* King, of Dunbar (1955) from Greenland) make no mention of either a much thickened pedicle umbo or lirate surface.

From *Spiriferellina* it is readily distinguished by its proportionately narrower sinus and fold, narrower more numerous plicae, median plica in the sinus, and lirate rather than spinose ornament. *Punctospirifer* also has sharper cardinal ridges, and differs further in the absence of fine regular growth-lines in addition to the growth lamellae, the absence of a plication in the sinus, the absence of strongly thickened umbonal

cavities in the pedicle valve, the lack of the strong convex thickening occupying most of the delthyrium, and the presence of a strongly protruding cardinal process.

I have not found species referable to this genus anywhere in the literature.

Liriplica alta sp. nov.

Plate 53, figs. 9–18

Holotype. F.4884; paratypes F.4885–F.4887, F.4891B, F.4892A–B, F.4893A–E, F.4894B, and F.4895G–L, from the uppermost fossiliferous bed near 019840.

Description. Shell approximately as long as wide; hinge-line less than the maximum shell width throughout ontogeny; cardinal extremities rounded; cardinal area high and strongly concave; umbo pointed; delthyrial angle averages 35° ; narrow shallow sinus extends the length of the valve, and within it a distinct median plica reaches to within 1 cm. of the umbo; lateral slopes well rounded and curve around on to the distinct but obtuse cardinal ridges, which become progressively sharper towards the cardinal extremities; lateral slopes each carry six or seven well-rounded plications; surface of each valve crossed by very fine closely spaced growth-lines, and at irregular intervals by much larger growth halts; fine radial lirae numbering twelve to fifteen per mm. in the sinus, well developed over whole surface except cardinal areas; lirae not similar in size, the largest being twice the size of the smallest; on adjacent lamellae, lirae appear to be in line.

Brachial valve much less convex than the pedicle; rather evenly convex in longitudinal profile, and gently convex on the lateral slopes; fold evenly rounded on the posterior half of the shell but develops a shallow median furrow on the anterior half; cardinal ridges curved toward the umbo, but become straighter laterally; size and spacing of punctae as in the generic description.

Pedicle interior with excessively thickened umbo and umbonal cavities; thickening continued well forward inside cardinal area, and a thick rounded ridge protrudes slightly anterior to hinge; this ridge arises from the sides of the dental lamellae, and runs outward and slightly forward, petering out before reaching lateral margins of valve; dental lamellae very swollen on their inner surfaces and fill the delthyrial cavity to varying degrees; median septum high and blade-like, arising from the muscle field at a very sharp angle; septum 1–2 mm. in width at base, and extremely variable in transverse section; in juvenile specimens septum passes backwards into narrow rounded callus partly filling apex of delthyrium, but this continuity obstructed in adults due to merging of callus with inner swollen edges of dental lamellae; extent to which delthyrium obstructed by callus variable, but usually one-half to two-thirds of its length; muscle field long and narrow, width/length ratios ranging from 0.4 to 0.55; adductor scars apparently sometimes restricted to sides of septum, but often occupying flattened area along its margins as well; few coarse genital pits scattered within 5 mm. in front and at the side of muscle field; hinge line not denticulate.

Brachial valve much thickened across shoulders; sockets small and shallow, and open over their entire length; socket plates thick, and buttressed by shoulder thickening; crural plates short and not attached as septa to floor of valve, their dorsal edges being deflected inwards and becoming confluent immediately beneath the umbo, forming a shelf on which the cardinal process is developed; cardinal process concave on ventral face; central adductor scars short and situated well forward (c. 5 mm. long in valve

22 mm. long, and their posterior edge *c.* 8 mm. from tip of umbo); scars restricted to median fold, broadest *c.* 1–2 mm. from their anterior extremity and taper gently backwards; postero-lateral adductor scars often on narrow sharp ridge near front, becoming broader and flat toward rear, and usually reaching to within 1 mm. of edge of crural plates; rear edge of these scars sometimes encroaching on first lateral plica; myophragm present.

Remarks. The callus occupying the delthyrium is very distinctive. Its outer surface is well rounded, and is either simple or divides into two toward the hinge-line. Usually its surface is not protruded beyond the plane of the cardinal area, but occasionally it is. In external view it is sharply separated from the inner faces of the dental lamellae by deep angular grooves. The muscle field and septum of the pedicle valve are highly variable. In some individuals there is a clearly defined trough on either side of the septum, presumably for the attachment of the lateral parts of the adductors. In other specimens there is no sign of these. Some of the variations in the longitudinal profile of the septum are given in text-fig. 3.

I know of no species to which *L. alta* is related.

Genus SPINULIPICA gen. nov.

Type species *Spinulipica spinulosa* sp. nov., Booral Formation.

Diagnosis. Shells of medium size; hinge-line less than maximum shell width at all growth stages; umbo low to moderate in height; pedicle cardinal ridges distinct but obtuse; lateral slopes with six or seven well-rounded costae; median sinus much broader than the bordering costae, and carrying a low median plication; surface of both valves crossed by fine growth-lines and coarse irregularly spaced growth halts; closely spaced, fine, anteriorly directed spines cover whole surface; dental lamellae strong and diverging down margins of sinus; median septum massive; umbonal cavities only slightly thickened; crural plates strong and frequently uniting with wall of shell to form short septa; cardinal process deeply platy, and supported on a thickening between the crural plates; adductor scars of brachial valve as in *Liriplica*; punctae number twenty to forty per sq. mm. and are irregularly arranged; in inner shell layer diameter of punctae is 0.03 to 0.07 mm.

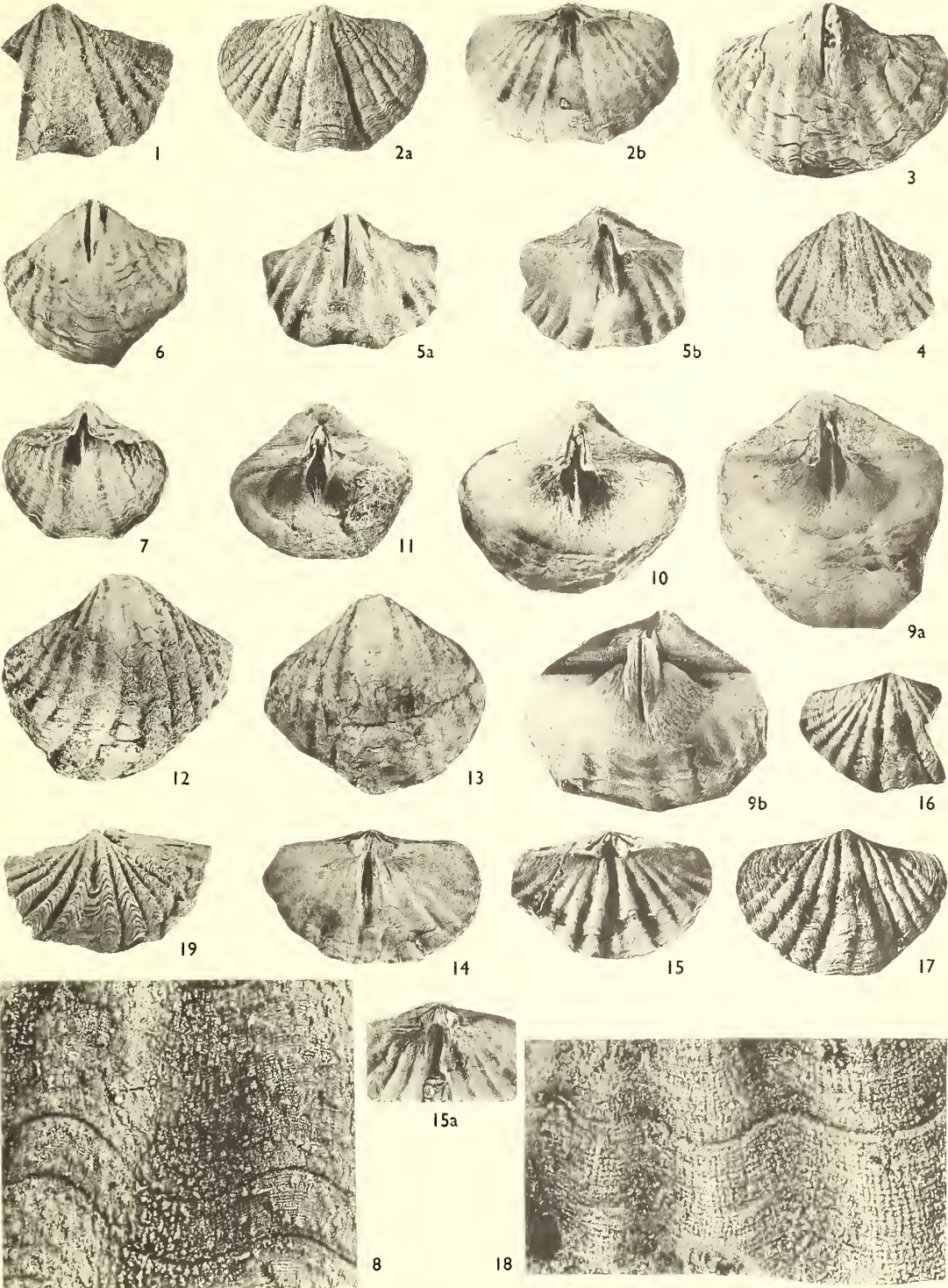
EXPLANATION OF PLATE 53

All figures natural size, and of rubber casts unless otherwise stated.

Figs. 1–8. *Spinulipica spinulosa* sp. nov. 1, 4. Exteriors of pedicle valves, F.4934D, and F.4934A. 2a–b, Exterior and interior of brachial valve, F.4931. 3, Mould of interior of pedicle valve, F.4922, holotype. 5a–b, Mould and rubber cast of interior of pedicle valve, F.4934B. 6, Internal mould of pedicle valve, F.4925. 7, Interior of small pedicle valve, F.4928A. Cardinal area slightly depressed into the shell. 8, Detail of surface ornament, F.4932A, $\times 10$.

Figs. 9–18. *Liriplica alta* sp. nov. 9a–b, Rubber cast and original internal mould of interior of pedicle valve, F.4885. 10–11, Interiors of two incomplete pedicle valves. Anterior parts of shell broken away. F.4893D and F.4894B. 12–13, Two pedicle valves F.4886 and F.4884. The latter is the holotype and is not a cast. 14–15a, Interiors of three brachial valves, F.4895G, F.4893B, and F.4887. 16–17, Brachial exteriors, F.4888B and the latter destroyed by fire. 18, External mould, showing details of ornament, F.4893J, $\times 10$.

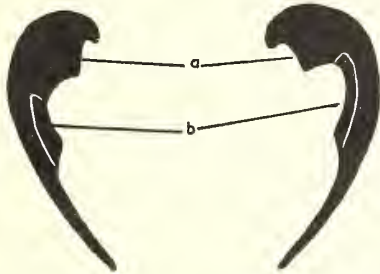
Fig. 19. *Punctospirifer* sp. Pedicle valve with umbo and part of brachial valve showing behind, F.4866.



Remarks. The appearance of the crural plates as septa is probably to be correlated with the absence of thickening in the umbonal cavities of the brachial valve. Where the thickening is strongest the crural plates are buttressed by it and do not appear as septa.

The genus is distinguished from *Liriplica* by its lower pedicle umbo, much less thickened pedicle valve, no distinctive callus between the dental lamellae and obstructing the delthyrium, and the presence of spines rather than lirae on the surface. *Spiriferellina* is smaller in size, has proportionately larger plicae in relation to the fold and sinus, and different fine surface ornament. *Punctospirifer* differs in its more extended hinge, non-plicate, fold and sinus, much higher cardinal area, and its lirate rather than spinose surface ornament.

Spiriferellina neerkolensis Maxwell possibly belongs to this genus, though spines have never been described on its surface, and the number of lateral plicae is fewer than in the type species.



TEXT-FIG. 3. Longitudinal sections of the pedicle valve of *Liriplica alta* gen. et sp. nov. showing the form of the umbonal callus and the median septum, together with the shape of the delthyrial cavity. The anterior third of each shell is partly reconstructed. $\times 1$. a, umbonal callus; b, median septum.



TEXT-FIG. 4. Longitudinal section of the pedicle valve of *Spinuliplica spinulosa* gen. et sp. nov. showing the form of the umbonal callus and the median septum, together with the shape of the delthyrial cavity. $\times 1$. a, umbonal callus; b, median septum.

Spinuliplica spinulosa sp. nov.

Plate 53, figs. 1-8

Holotype. F.4922; *paratypes* F.4923-F.4928A from beds below the main *Levipustula* bed near 019840, and F.4934A-D from near 018859.

Description. Shell slightly wider than long at adult stage, and hinge-line less than maximum width of shell at all growth stages; young forms with rather well-rounded cardinal extremities, but adults show a slight tendency to become subrectangular; cardinal area of moderate height and strongly concave; sinus twice to three times width of bordering plicae, and contains a median plication which does not quite reach the umbo; on some specimens this plication fades away on anterior part of sinus, which then becomes flat bottomed; lateral slopes well rounded and carry six or seven well-rounded plicae separated by furrows of similar size and shape.

Brachial valve flatter than pedicle; umbo rather prominent; fold not very high and carries a distinct median furrow almost to umbo.

Surface of both valves crossed by very fine, delicate growth-lines and coarse irregularly

spaced growth halts, closer together towards front of shell; very fine, hollow, irregularly spaced spines cover surface, both on and between plicae, and in sinus; spines derived from anterior edges of elongate bases which gradually increase in height forwards; spine bases range up to 1 mm. in length, and adjacent ones about 0.1–0.4 mm. apart; spines probably no more than 2 mm. long.

Dental lamellae thick and supported on short thick wedge-shaped adminicula which diverge along margins of sinus; median septum very powerful, broadly based on floor of valve, and usually arises abruptly from diductor field, though sometimes with a gradual change of slope at its base; septum in transverse section irregularly triangular, though occasional specimens show a vertically walled lower portion capped by a triangular crest; maximum height of septum at a distance of 3–5 mm. from its anterior edge, towards which it then falls away on a concave slope; umbonal cavities relatively unthickened.

Crural plates thick, with their inner edges curved around and buried in callus supporting cardinal process; in some specimens crural plates unite with the outer wall of the valve to form septum-like structures; very weak myophragm; adductor scars as in *Liriplica*.

Remarks. There is some variation within this species at different localities within the formation. Particularly noticeable is the variation in the thickening of the pedicle umbo and the umbonal cavities, though even the most thickened individuals never approach the form of *Liriplica*.

The spines are preserved as moulds in mudstone and are pressed fairly closely to the shell. They are not completely tubular, but appear to be more or less cylindrical with a slit along the face adjacent to the shell. Some individuals appear to be tubular immediately adjacent to the shell wall but then split distally.

The species is widely distributed in both sandy and muddy facies, but has not been found in the *Liriplica* bed at the top of the fossiliferous section.

Genus PUNCTOSPIRIFER North 1920

Type species *P. scabricosta* North from the Lower Carboniferous of England.

? *Punctospirifer* sp.

Plate 53, fig. 19

Material. F.4866; from beds below the main *Levipustula* bed near 019840.

Description. Shell transverse, length about two-thirds width; cardinal extremities rounded in earliest stages, then acute, then mucronate, and finally acute again; pedicle umbo of moderate height, pointed and apparently only slightly incurved; sinus with a rounded to slightly flattened base; lateral slopes each with five strong rounded plicae, separated by sharp, subrounded interspaces; lamellae very strong and imbricating; fine radial lirae over whole surface.

Remarks. Only one specimen of this species has been found. It consists of an external mould of the pedicle valve and the internal mould of part of the corresponding brachial valve. The margins of the pedicle valve have been destroyed, but the form of the cardinal extremity has been preserved in the brachial valve. The external mould is covered with

small pustules which are, no doubt, the infillings of the punctae from the outside. Between these, and on the small areas where they are not developed, the surface is very delicately lirate.

I am referring this form to *Punctospirifer* because of its form and the details of its surface ornament. However, it differs from the type species in its fewer plications, and the relatively smaller sinus. Definite assignment to a genus is not possible without knowledge of the internal structures.

Subfamily SYRINGOTHYRINAE Schuchert and Le Vene 1929

Genus SYRINGOTHYRIS Winchell 1863

Type species *Syringothyris typa* Winchell, Lower Mississippian Burlington Limestone, Burlington, Iowa.

Remarks. There is some doubt as to the correctness of this generic assignment for the following reasons. (1) The sinus has furrows developed on its lateral parts. (2) The cardinal area of the pedicle valve appears to be vertically striated over its entire width. (3) The postero-lateral adductor scars are distinctly bifid. (4) The apical part of the syrx is joined to the floor of the valve by a short 'euseptoid'. In this feature it resembles *Septosyringothyris* Vandercammen, but the other characters prevent it being placed in that genus.

? *Syringothyris bifida* sp. nov.

Plate 62, figs. 1–9, and Plate 63, fig. 5

Holotype. F.4917A; paratypes F.4909–F.4914A–E, F.4915E–G, and F.4916A, from the Isaacs Formation near 987823.

Description. Shell very transverse, being *c.* 1.75 times wider than long in adults though beyond a certain stage there is a marked allometric increase in length with respect to width; cardinal extremities subangular; apical angle varies from about 130° to 140°.

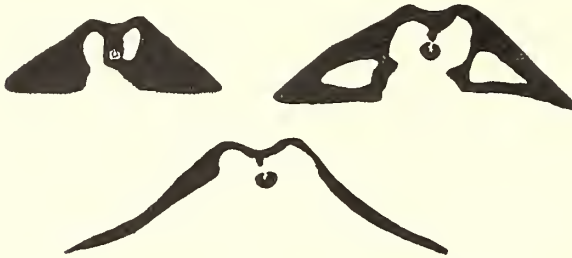
Length of cardinal area of pedicle valve between one-third and one-half of the total length of the shell; area gently and evenly concave over its entire length, in lateral profile forming a quadrant of a circle; delthyrial angle about 40°–45°; cardinal area appears to be vertically striated over its whole width, though the preservation is such that it is impossible to be certain of this; sinial angle from 16° to 35°; diverging from the margins of the sinus at a low angle are two shallow furrows which extend to the anterior margin, the first arising *c.* 5 mm. from the umbo and the second *c.* 10 mm.; lateral slopes with from sixteen to eighteen simple, low, rounded plicae, separated by furrows narrower and more angular than themselves.

Brachial valve only moderately convex; cardinal area 3–4 mm. high in valves 25 mm. long, and 5–6 mm. high in 45 mm.; fold high, with rather flat flanks, rounded crest posteriorly, and slightly furrowed medially over most of its length; lateral parts of flanks occasionally showing a single faint furrow.

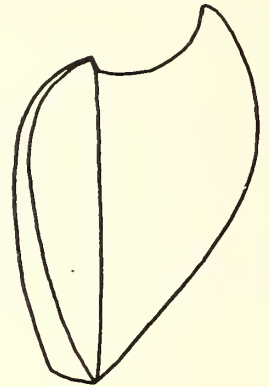
Surface of both valves, except for cardinal areas, covered with very fine elongate depressions, varying in length from 0.1–0.7 mm., and also varying in density; shell substance punctate, but density of punctae unknown.

Dental lamellae stout, but shallow, e.g. in specimens with cardinal areas *c.* 20 mm.

high, maximum depth of the dental lamellae (near their mid-length) is only c. 4 mm.; adminicula short, very strongly thickened, very widely divergent, and largely embraced in the extensive umbonal thickening; solid transverse plate closes only posterior third of delthyrium, in some cases a little more; outer surface of plate convex, and in most specimens with a low, rounded to angular, median ridge; well-developed syrnix with diameter of up to 6 mm. and length of up to 15 mm. measured from the tip of the umbo, though in most specimens diameter c. 3 mm. and length c. 10 mm.; syrnix projects well beyond edge of transverse plate, and split on its ventral face; inner surface of syrnix connected to floor of valve by a stout euseptoid; muscle field very large



TEXT-FIG. 5. Three sections across the pedicle umbo of *Syringothyris bifida* sp. nov. showing the relation of the syrnix to the septum. The specimen, F.4913, is partly in the form of a mould and the external surface of the shell has been reconstructed. The intervals are approximately 3 mm. and 2 mm. respectively. $\times 1$.



TEXT-FIG. 6. Reconstructed lateral profile of *Syringothyris bifida* sp. nov. $\times 1$.

and circumscribed by a low ridge increasing in height with age; adductor scars smooth, canoe-shaped in outline, and bounded by a very low, narrow, sharp ridge; posterior extremity of adductors situated c. 5–9 mm. in front of posterior edge of diductors, and their anterior extremity at or up to 3 mm. behind the edge of the field; broad diductor scars invariably exhibit a very delicate arrangement of ribbing, with pattern as follows: on anterior two-thirds ribs run anteriorly and antero-laterally, and on posterior third, separated by a sharp break in direction of ribs, they run laterally, or laterally towards the front and postero-laterally towards the rear; coarse genital pits on inside of cardinal area, beside muscle field, and occasionally forward of cardinal ridges.

Large callus immediately beneath the umbo of brachial valve bearing large deeply striate cardinal process 5–6 mm. broad and 2–3 mm. long in adults; crural plates broad and lying at a low angle to the general plane of the cardinal area, and with their posterior portions incorporated in the umbonal callus; ventral faces of crural plates slightly excavate and with their inner edges deflected ventrally; socket plates slightly thickened, and form a low rounded ridge where they attach to the shell wall forward of the hinge-line; no material preserving brachidia available; central pair of adductor scars situated with its posterior edge 15–20 mm. from umbo (measured around the curvature of the shell, in valves 40–50 mm. long), and scars themselves c. 23 mm. long; outline elongate oval, expanding slightly forwards, and situated on crest and flanks of fold; postero-lateral scars sharply bifid, reaching to within 3–7 mm. of anterior edge of

central pair, with their outer edges curving backwards in a broad arc, extending laterally on to the second costa lateral to the fold, and posteriorly to within 3–6 mm. of edge of umbonal callus; division in these scars 8–10 mm. from their posterior edges; straight inner segments run backwards along depressions bounding fold, and adjacent to central pair of scars; all scars slightly impressed, the degree of impression increasing posteriorly; very low myophragm flattens out into umbonal callus, or stops short of it; numerous fine, radial markings at anterior edge of fold.

Remarks. Sections from a testiferous specimen show structures very closely comparable with those figured by Amos (1957) for *Septosyringothyris* aff *keideli* Harrington both as regards the 'euseptoid' and the syrx. In my internal moulds the 'euseptoid' varies considerably in strength, in some being virtually absent. This is no doubt due to the excessive deposition of callus around it. *S. bifida* differs in the form of the cardinal area of the pedicle valve, the more numerous lateral plicae, and the presence of furrows in the sinus. Amos (pers. comm.) informs me that his specimens are decorticated and that this may account for the apparent smoothness of the sinus. In 1958 the same author figured two poorly preserved specimens from the upper (Moscovian?) part of the Sistema de Tepuel as *S. keideli*.

The types of *S. keideli* compare very well with *S. bifida* in general form, size and disposition of the pedicle cardinal area and ornament. Further, Harrington has noted 'faint longitudinal rounded striae marking the surface of the sinus', in the only specimen in which the outer shell layers are preserved. The chief difference is the smaller number of plicae on the lateral slopes of *S. bifida*.

Specimens from the Moscovian part of the Agglomeratic Slate of Kashmir referred by Bion (1928) to *Syringothyris lydekkeri* (Diener) have a very similar form to this new species, and there is a similar arrangement of the dental lamellae and adminicula, but there appears to be no 'euseptoid' in the pedicle valve. Other critical details are wanting. It is interesting to notice that the pedicle cardinal area of the same species figured by Diener (1915, pl. 4, fig. 4) from the *Fenestella* Shales—a slightly earlier formation—seems to be vertically striated over its whole surface.

I can find no reference to comparable species from Europe or North America.

Superfamily ROSTROSPIRACEA Schuchert and Le Vene 1929

Family ATHYRIDAE Davidson 1884

Genus COMPOSITA Brown 1849

Type species *Spirifer ambiguus* Sowerby, Lower Carboniferous, England.

Remarks. This genus has been discussed previously by the author (1953, p. 15) in connexion with its differentiation from *Spirigerella* Waagen. As stated there, Grabau (1932) claims that *Spirigerella* has a large cardinal process which projects into the umbo of the pedicle valve, but no such structure is present in *Composita*. If this is a reliable basis for distinction, then the new species here described is clearly a *Composita* since no cardinal 'process' is developed at all, the diductor muscles being attached to the cardinal plate.

So far as I am aware this genus has not been recorded as such from the Carboniferous of eastern Australia, but Benson and Dun (1920) have referred specimens from the Tournaisian at Babbinsboon to *Seminula subtilita* (Hall), which is a species of *Composita*.

However, these specimens appear to be incorrectly assigned. The incoming of this genus may prove to be a useful indicator in the Carboniferous of New South Wales and Queensland.

Composita magnicarina sp. nov.

Plate 55, figs. 1-8

Holotype. F.5276; *paratypes* F.5277-F.5278; from the Booral Formation near 018859.

Description. Shell of small to average size for the genus; width from two-thirds to four-fifths of the length; maximum width at two-thirds the length from the umbo; postero-lateral margins very gently curved to the point of maximum width and the anterior outline approaches a semicircular form; valves subequally convex.

Pedicle umbo gently incurved over its brachial counterpart, with its apex occupied by a small foramen *c.* 1.5 mm. in lateral diameter; foramen not complete but opens into the broad, open delthyrium; median sinus variable, ranging from virtually absent to a shallow rounded depression which originates variously at points between the middle of the valve and 2 to 3 mm. in front of the umbo; many specimens with only a mesial flattening; commissure only gently plicate, the fold being of the order of 2 to 4 mm. in height in adults; lateral slopes gently rounded.

Umbo of brachial valve high and acute and fits right into the delthyrium; valve either gently rounded or slightly flattened medially; surface of both valves crossed only by very fine, rather regular lines of growth.

Dental lamellae strong and reach one-third the total length of the valve, their inner surfaces distinctly concave and they thicken greatly towards the teeth; along floor of valve dental lamellae almost straight or only slightly divergent; almost whole floor of delthyrial cavity as far forward as anterior edge of dental lamellae occupied by a very finely concentrically striated pedicle muscle scar; adductor scars elongate cordate in outline and occupy one-half to two-thirds of total length, and one-third to one-half of total width, of muscle field; outer edges of diductor scars diverge slightly forwards for a little more than half their length and then converge to give a bluntly rounded anterior termination; posterior edges of diductor scars lie between tips of dental lamellae or just anterior to them.

Hinge-plate thick, its length from the umbo being one-fifth of the total length of the valve, and directed antero-ventrally; crural bases form low ridges just within the inner socket ridges; centre of plate forming a shallow trough with a low axial fold; apex of plate in juveniles with a small foramen which sometimes remains open and sometimes is closed by a callus in adults; largest foramen observed 1.7 mm. in length; diductor attachments a pair of slightly flattened areas one on each side of foramen; strong broad-based and sharp-crested median ridge arises just in front of umbonal opening, reaches its maximum height and width within 5 mm., and then usually tapers gradually to middle of valve; in some specimens, however, decrease in size not gradual but sharp, either where the septum enters the adductor field or where it reaches the rear end of the anterior pair of scars; median ridge never supports hinge-plate; adductor scars situated in a narrow shallow depression on either side of median ridge; posterior pair usually well impressed at rear edge which is situated 3 to 4 mm. from the tip of the umbo in adults, but it is usually very difficult to distinguish sharply between posterior and anterior pairs; when distinguishable, pairs are of about the same length; usually anterior

and posterior scars approximately equal in width, but sometimes posterior pair up to twice the width of the anterior, and sometimes anterior pair slightly the wider; front edge of muscle field tapers to an acute termination from which a pair of short pallial trunks is derived; posterior portion of valves sometimes with a few small, radially elongate genital pits; jugum not observed; about twelve volutions in each spire, the coiling being of the normal type for the genus (see Kozłowski 1914).

Remarks. This species occurs at almost all localities, and on several levels, in the Booral Formation. It is most abundant, however, on the lower horizons. The specimens from the finer sediments to the south of the highway are much larger in size and more variable internally than those from the type locality, and, in addition, they have some distinctive features. The dental lamellae are usually slightly longer, being somewhat more than one-third of the total length of the valve. The hinge-plate is usually more strongly thickened, and in some specimens it becomes ponderous. The median carina is often very broad and high and occasionally it supports the hinge-plate for a short distance beneath the umbo, but other specimens have exceptionally weak carinae. It is probable that the forms from the two types of sediment are phenotypic variants.

Composita sp.

Material. F.4979–F.4984 from the Isaacs Formation near 987823.

Remarks. These specimens are rather badly distorted, but sufficient details can be determined to separate them from *C. magnicarina*. They are more transverse in outline, have thinner shell material, and usually have a very weak median keel in the brachial valve.

Suborder TEREBRATULOIDEA Muir-Wood 1955

Superfamily TEREBRATULACEA Waagen 1883

Family DIELASMATIDAE Schuchert and Le Vene 1929

Subfamily? CRYPTONELLINAE Thomson 1926, emend. Cloud 1942

Genus BOORALIA gen. nov.

Type species *Booralia ovata* sp. nov. from the Booral Formation.

Diagnosis. Dielasmatids with ovate outline, and rectimarginate to slightly sinuate commissure; deltidial plates large and conjunct; cardinal 'process' flattened or more commonly bearing a globular median eminence; cardinal plate deeply concave and perforate; crural bases low; loop unknown; dental lamellae long; pedicle collar on dorsal side only, where it is buttressed against the deltidial plates by a short septum; foramen of moderate size, mesothyrid to submesothyrid; muscle scars of pedicle valve poorly defined, and adductor scars of brachial valve club-shaped; two pairs of divergent pallial trunks in each valve; punctae twenty to forty per sq. mm., and are c. 0.02–0.03 mm. in diameter in the inner shell layer.

Remarks. In the absence of any knowledge of the loop, it is difficult to know whether this genus is a cryptonellinid or a cranaeninid. From a stratigraphic point of view the latter appears to be the more likely, since members of that subfamily range up to the top of the Mississippian, whereas those of the former are probably restricted to the Devonian, though Cloud suggests that the Pennsylvanian *Cryptacanthia* may possibly

be a cryptonellid. However, from a morphological point of view *Booralia* seems to be closer to *Cryptonella* than *Craenaena* in its relatively long suberect to nearly straight beak, and its mesothyrid to submesothyrid attrite foramen. A further point of similarity is in the pattern of pallial trunks in the brachial valve. Cloud (1942, pl. 24, fig. 27) has figured pedicle and brachial interiors of a *Craenaena* or a *Hamburgia* which show the pallial pattern of the subfamily. In the brachial valve there appear to be four large straight trunks on either side of the mid-line. Cloud's description of the trunks in *Cryptonella* fits the pattern in *Booralia*.

Booralia is distinguished from all other members of both subfamilies by the presence of the long dorsally placed pedicle collar which is attached to the deltidial plates, and by the distant irregular spacing of the punctae.

Booralia ovata sp. nov.

Plate 55, figs. 9–16

Holotype. F.4892C; and paratypes F.4888–F.4891A, F.4893F–G, and F.4895G–L, from the *Liriplica* bed near 019840; paratypes F.4896–F.4901 from sandy bed near 018859.

Description. Pedicle valve moderately convex in longitudinal, and highly arched in anterior profile; outline elongate with umbonal angle between 80° and 90° ; maximum width just forward of umbonal ridges; outline of anterior well rounded; umbo suberect to nearly straight; cardinal margin terebratulid; foramen of moderate size—c. 2 mm. across in specimens 30–40 mm. long—and mesothyrid to submesothyrid; foramen margin attrite; umbonal ridges subangular; surface smooth, without a sinus; commissure either rectimarginate or slightly sinuate; deltidial plates large and conjunct.

Brachial valve flatter than pedicle; umbo high and blunt; no fold; surface smooth.

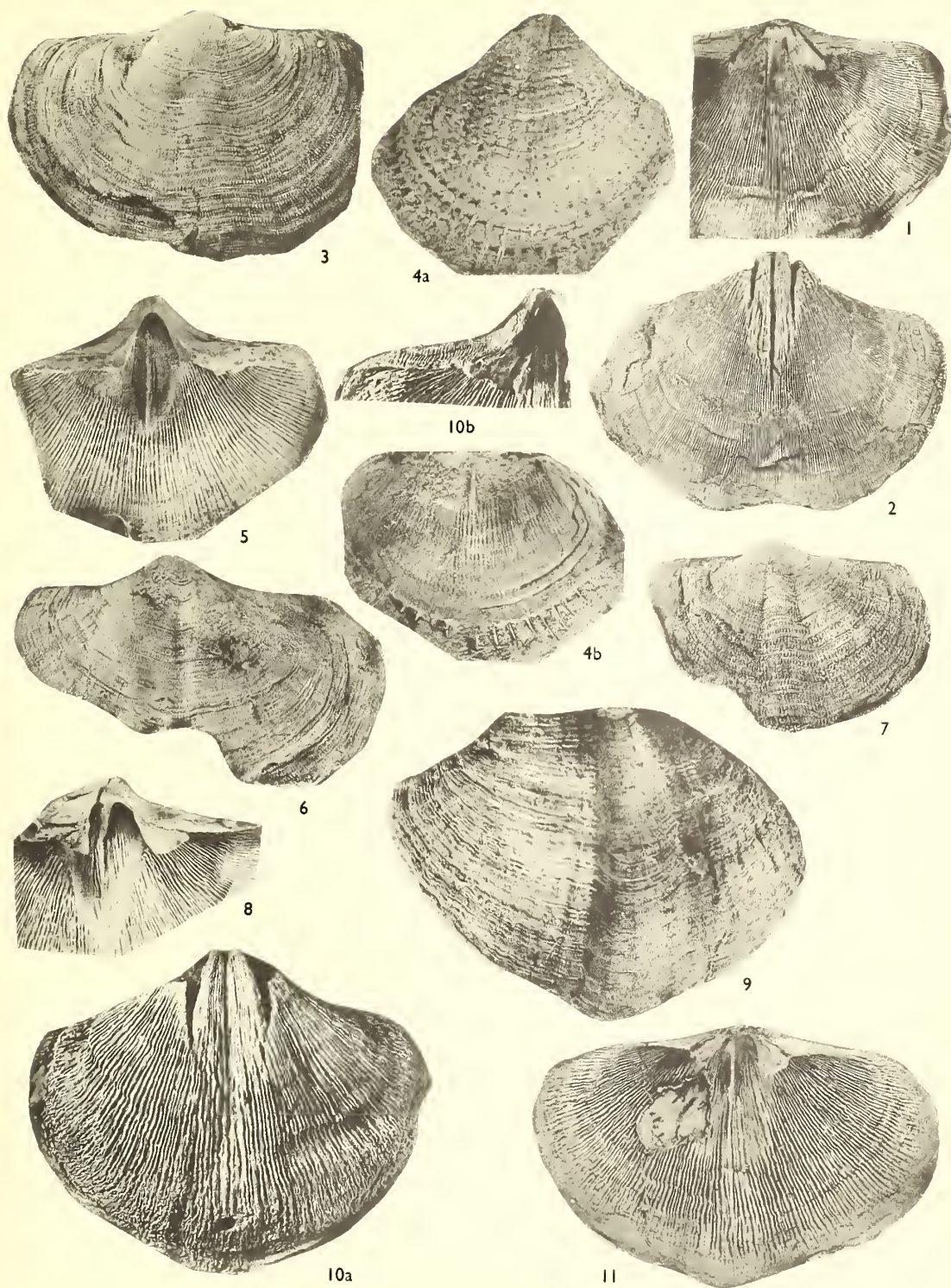
Dental lamellae strong, about one-third the length of the valve, strongly concave toward each other in transverse sections, straight along the floor of the valve or slightly incurved at their anterior tips; shell substance within delthyrial cavity slightly thickened, the anterior edge of the thickening forming a slight, arcuate ridge between the tips of the dental lamellae; pedicle adjustor scar in delthyrial cavity; adductor scars very poorly defined; relatively small lateral pair subovate and lying within strong pallial trunks diverging from the inner anterior edges of the dental lamellae; median pair of adductor scars not observed; lateral pallial trunks diverge from outside dental lamellae; pedicle collar developed on dorsal side only where it forms a sheath inside the delthyrium; collar and deltidial plates joined by a short septal plate.

EXPLANATION OF PLATE 54

All figures natural size, and of rubber casts unless otherwise stated.

Figs. 1–3. *Phricodothyris booralensis* Campbell. 1, 3, Interior and exterior of brachial valve, F.4902A–B. 2, Internal mould of pedicle valve, F.4903A, neotype.

Figs. 4–11. *Phricodothyris immensa* sp. nov. 4a–b, Exterior and interior of pedicle valve, F.4939A–B, $\times 4.5$, showing fringe of spines. 5, Interior of pedicle valve, F.4918. 6, Exterior of pedicle valve, F.4915b. 7, Exterior of small brachial valve, F.4914g. 8, Slightly oblique view of interior of posterior part of pedicle valve showing septum joined to ridges on inner faces of dental lamellae, F.4919. 9, Part of exterior of pedicle valve showing faint plication of surface, F.4914f. 10a, Internal mould of pedicle valve, destroyed by fire. 10b, Rubber cast of part of same showing denticle grooves on cardinal area. 11, Interior of brachial valve, F.4917c, holotype.



Cardinal plate short, free, perforate and deeply concave, its anterior edge concave forwards; crural bases distinct, sharp and running well back on to the plate; sockets large and socket plates short, very robust and joined to the outer wall of the shell by massive callus deposits making the posterior part of the shell very solid; myophores form flattened areas immediately forward of the umbo, or more frequently situated on a globular eminence sometimes of considerable size; two strong, broad, parallel



TEXT-FIG. 7. Two semi-diagrammatic sections across the umbonal region of *Booralia ovata* gen. et sp. nov., drawn from F.4901, an internal mould approximately 25 mm. long, the sections being taken 4 mm. apart. $\times 5$. a, pedicle collar; b, septum joining pedicle collar to deltidial plates.

ridges, separated only by a narrow furrow, proceed from under the cardinal plate to a point about one-third the length of the valve from the umbo, and then diverge, making angles $c. 25^\circ$ with each other, presumably marking sites of pallial trunks; lateral trunks slightly concave towards mid-line, and diverging from central pair near edge of cardinal plate; adductor scars club-shaped, depressed, situated between median ridges and lateral pallial trunks, though usually partially encroaching on the former to a variable degree; lateral and central adductor scars not clearly differentiated; anterior edge of scars at or just on either side of separation of central pallial trunks.

Remarks. The specimens from the crinoidal bed (*Liriplica* bed) are large and have well-impressed internal structures, but most of them are fragmentary. Those from the sandy beds are very much smaller (? younger) and do not show the internal structures well, though they are sometimes preserved as complete internal and external moulds. I have considered the possibility that the two forms are distinct species, but for the present consider them to be phenotypic variants.

The cardinal process is a very variable structure. Almost all the large well-preserved specimens have the pronounced boss in the middle of the face of the cardinal process, but the smaller specimens from the sandy beds do not. However, there is no boss in one of the largest specimens, and so apparently age is not the controlling factor.

The median ridges on the posterior third of the brachial valve are clearly not pallial trunks, but the central pair of trunks is always derived from their anterior edges.

Suborder RHYNCHONELLOIDEA Moore 1952

Superfamily RHYNCHONELLACEA Schuchert 1896

Family CAMAROTOECHIIDAE Schuchert and Le Vene 1929

Genus LISSELLA gen. nov.

Type species *Lissella booralensis* sp. nov., Booral Formation.

Diagnosis. Small, impunctate rhynchonelliform shells with smooth umbones; lateral slopes developing a small number of rounded plicae toward the front of the shell; median sinus and fold well developed and carrying few plicae; dental lamellae fine and short; hinge-plate robust, with a distinct median ridge on its ventral surface, and strong flanges on its dorsal surface giving rise to the crurae; median septum high and long, but never supporting the hinge-plate at any stage; small perforation in hinge-plate immediately in front of umbo; muscle scars in the brachial valve complex, consisting of four distinct pairs; teeth and sockets not denticulate.

Remarks. This genus bears obvious resemblances to *Wellerella* Dunbar and Condra in its size, shape, ornament, dental lamellae, undivided hinge-plate with its ventral median ridge and its dorsally placed crural bases. However, according to Dunbar and Condra 'The apical part of the hinge-plate (of *Wellerella*) is supported by a very short simple median septum', whereas *Lissella* has a long, high septum which does not support the hinge-plate at any stage, and the hinge-plate has a small apical perforation. Certain species from the Permian ascribed by Stehli (1954) to *Wellerella* have in the brachial

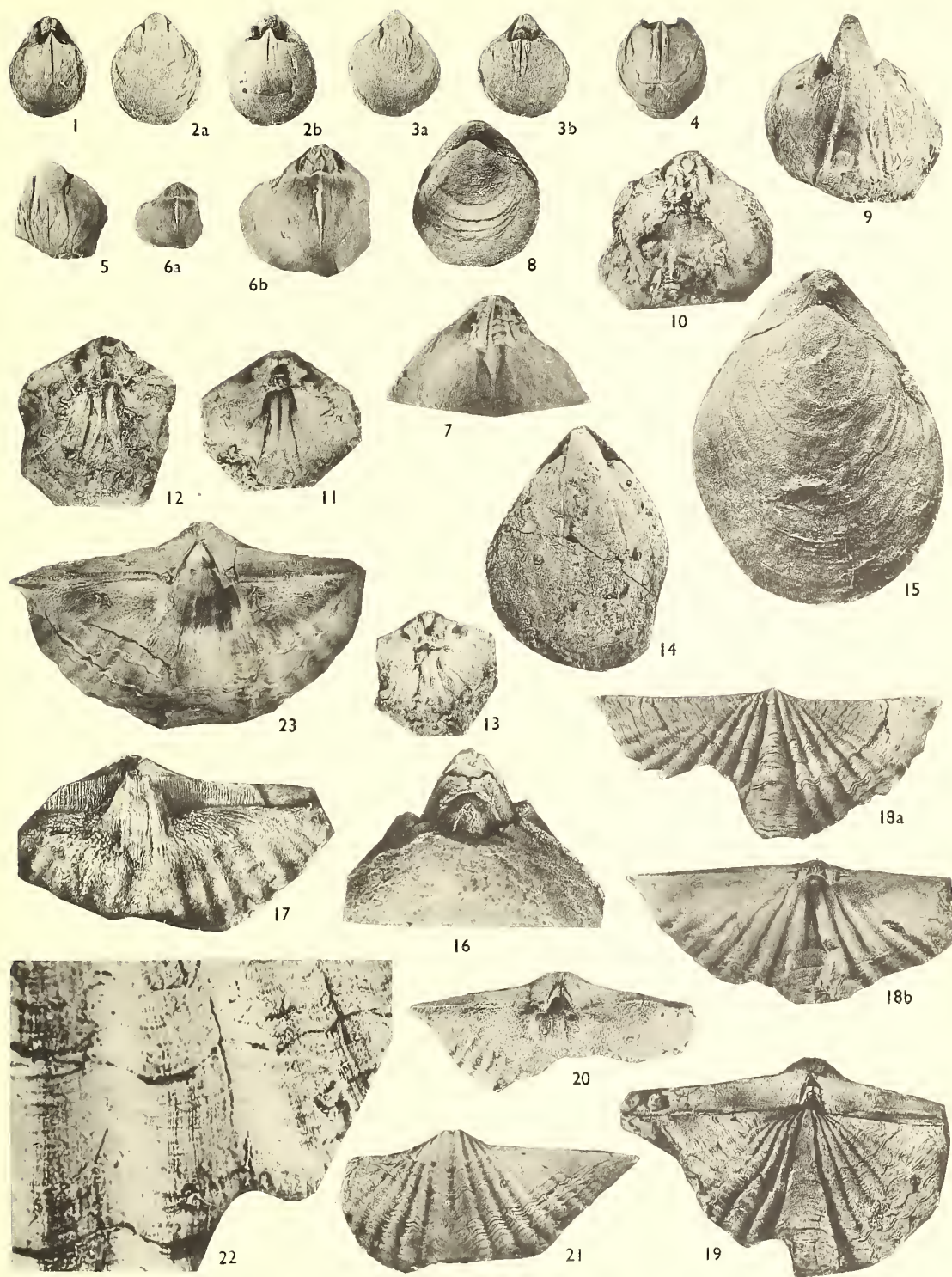
EXPLANATION OF PLATE 55

All figures are natural size unless otherwise stated.

Figs. 1–8. *Composita magnicarina* sp. nov. 1, Dorsal view of internal mould, F.5277. 2a–b, Ventral and dorsal views of internal mould, F.5278. 3a–b, Ventral and dorsal views of internal mould, F.5276, holotype. In 3b, the infilling of the brachial umbonal cavity has been cut away. 4, Brachial valve, internal mould, F.5300. 5, Umbonal part of internal mould of pedicle valve showing transversely striated umbonal cavity and adductor and diductor scars, F.5301. 6a, Rubber cast of interior of brachial valve showing hinge-plate and unusual myophores, F.5302. 6b, Same, $\times 2$. 7, Rubber cast of interior of brachial valve showing hinge-plate and socket, F.5303, $\times 2$. Slightly oblique view. 8, Rubber cast of exterior, showing foramen, F.4934f, $\times 2$.

Figs. 9–16. *Booralia ovata* sp. nov. 9, Internal mould of pedicle valve with front part destroyed, F.4895A. 10–13, Rubber casts of interiors of umbonal parts of brachial valves, F.4893f, F.4889, F.4892c, and F.4895h. Note presence of boss on cardinal 'process' in all except fig. 11. 14, Internal mould of pedicle valve with infillings of umbonal cavities broken away, F.4888. 15, Dorsal view of rubber cast of exterior, F.4889b, $\times 1.7$. 16, Dorsal view of internal mould with umbonal infilling cut away to expose cardinal 'process' and crural trough. Note crural base on left-hand side; strongly developed pedicle collar on dorsal side; and short septum connecting the pedicle collar to the deltidial plates, F.4898, $\times 2$.

Figs. 17–23. *Alispirifer laminosus* sp. nov. 17, Internal mould of pedicle valve, destroyed by fire. 18a–b, Rubber casts of exterior and interior of brachial valves, F.4945b and F.4941. 19, Rubber cast of exterior, F.4940a. 20, Rubber cast of pedicle interior, F.4938e. 21, Rubber cast of pedicle exterior, F.4940b. 22, Rubber cast showing details of surface ornament, F.4938a, $\times 7$. 23, Rubber cast of interior of pedicle valve, F.4938b, holotype. Note denticulation of hinge-line, delicate tracery of vascula genitalia, and large callus boss in delthyrium.



valve variable septa which support the hinge-plate for greater or lesser distances. The same author (1955) has commented on and illustrated Permian specimens of *Wellerella*? with very long brachial median septa, and denticulate teeth and sockets. Further, the adductor scars of the brachial valve of the Permian specimens have a very unusual and distinctive arrangement. If these characters, which at present are not known in the genotype, are eventually proved to occur in it, they will provide further satisfactory means of distinguishing it from *Lissella*.

In *Leiorhynchus* the median septum of the brachial valve supports the hinge-plate in the umbo, and a small crural cavity is present. Further, the sockets are denticulate, and the adductor scars of the brachial valve are somewhat differently placed, and hence these specimens seem to belong to an entirely different stock.

Lissella booralensis sp. nov.

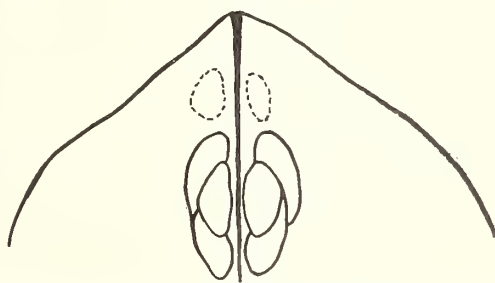
Plate 56, figs. 3-9

Holotype. F.5262; paratypes F.5263-F.5265 from the Booral Formation at 018859, and F.5268-F.5269 from the beds above the main *Levipustula* bed near 019840.

Description. Shell small, the largest one observed being only 16 mm. long; pedicle valve rather strongly convex near the umbo, but in general tends to be gently convex; postero-



TEXT-FIG. 8. Transverse sections across the brachial valve of *Lissella booralensis* gen. et sp. nov.; semi-diagrammatic, and reconstructed from sections of several internal moulds. $\times 3$.



TEXT-FIG. 9. Camera lucida drawing of the muscle scars in the brachial valve of *Lissella booralensis* gen. et sp. nov. $\times 3$.

lateral margins straight, and pass into a broadly rounded anterior; on anterior half to two-thirds of shell is a broad, rather shallow sinus, produced into a high tongue; umbonal region of lateral slopes smooth, but two or rarely three low rounded to subangular plicae (including the one bordering the sinus) developed anteriorly; median portion of sinus occupied by two, rarely one or three, rounded plicae not extending to umbo; deltidial plates narrow and short; foramen well rounded and relatively large.

Brachial valve strongly convex; lateral slopes steep; fold flat on top; plication in commissure high; usually three, sometimes two or four, rounded plicae on fold.

Pedicle valve with very delicate dental lamellae concave toward each other in transverse section and slightly divergent along the floor of the valve; lamellae extend one-sixth to one-quarter of total length of valve; arrangement of muscle scars unknown.

Brachial valve with a strong undivided hinge-plate with a minute perforation immediately in front of umbo; mid-line of hinge-plate with a low blunt ridge rising

gradually from the posterior and terminating much more abruptly anteriorly; crural bases strong, rather sharp, and situated on dorsal surface of hinge-plate; very strong median septum extends approximately half the length of the valve; septum never supports hinge-plate, though it comes very close to its dorsal face; near umbo septum very low and rounded but rapidly increases in height before reaching anterior edge of hinge-plate, maintains this height for some distance, and then gradually tapers to its anterior tip; muscle scars rarely visible, but on one specimen they are beautifully preserved (see text-fig. 9); socket plates strong; sockets not denticulate.

Remarks. This species occurs in considerable numbers on certain horizons of the Booral Formation but specimens are almost always grossly distorted. However, the sandy bed near 018859 has a large number of specimens well preserved as moulds. The specimens from the two types of sediment differ in that those from the mudstone usually have three to four plicae on the fold, and those from the sandstone have two to three.

The material is not well enough preserved to prepare accurate serial sections, but the internal moulds show the characters of the septum and hinge-plate very well.

Order CRYPTOSTOMATA Vine 1883
Family RHABDOMESIDAE Vine 1883
Genus RHOMBOPORA Meek 1872

Type species *R. lepidodendroides* Meek, Permian, America.

Remarks. These specimens are all preserved as moulds which are oval in cross-section, and at first it was thought that they had a similar cross-section to that of *Ottoseetaxis*. Mr. G. Fleming of the University of Queensland has shown me specimens from the

EXPLANATION OF PLATE 56

All figures are of rubber casts and are at natural size unless otherwise stated.

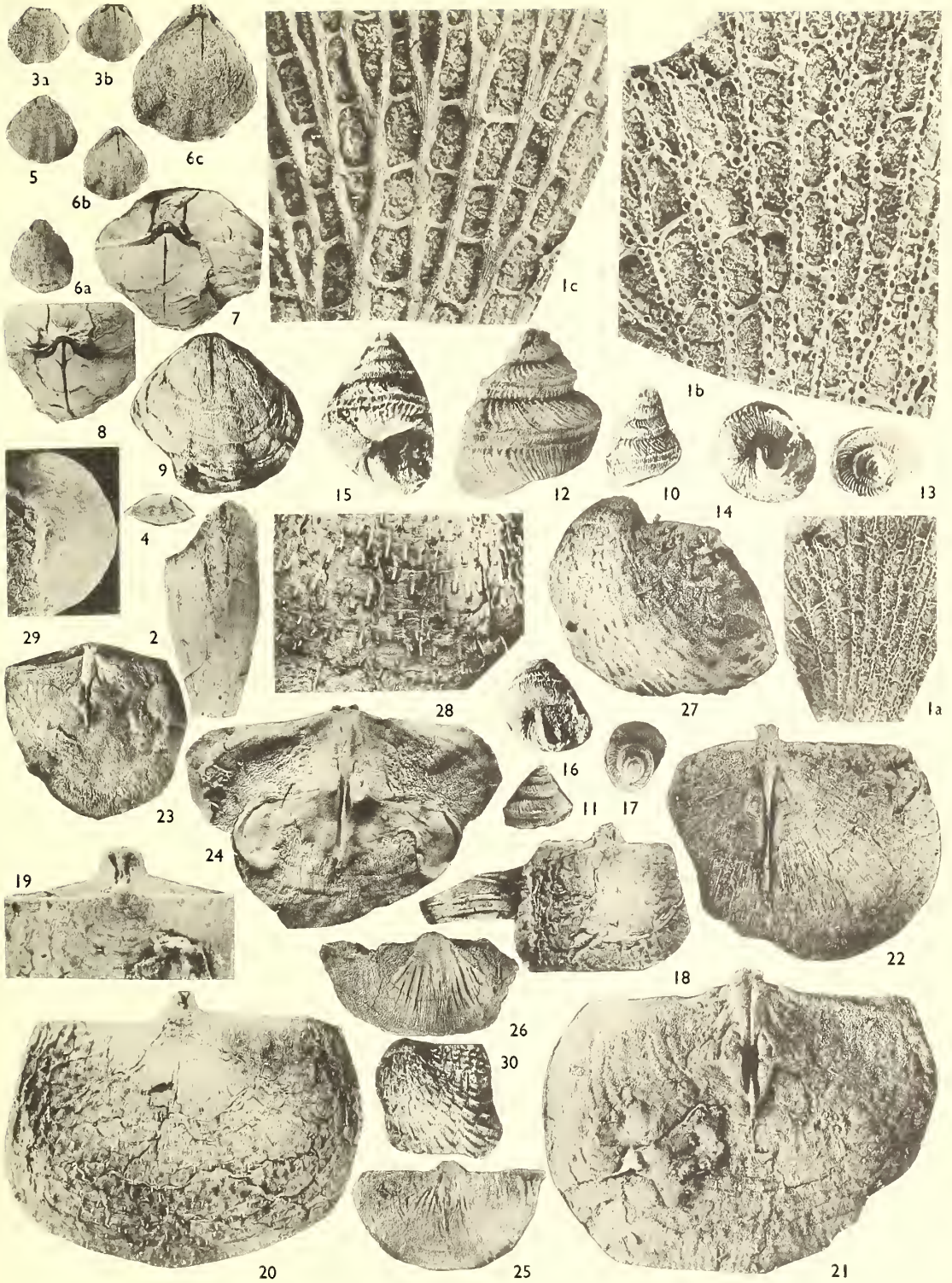
Fig. 1. *Fenestella stroudensis* sp. nov. 1a, Obverse surface, F.4704B, holotype, $\times 2.6$. 1b, Same, $\times 6.3$. 1c, Reverse surface, F.4704C, $\times 6$.

Fig. 2. ? *Pentremites* sp. Isolated plate F.4714C, $\times 2$.

Figs. 3-9. *Lissella booralensis* sp. nov. 3a-b, Ventral and dorsal views of internal mould, F.5264. 4, Anterior view of internal mould, F.5263. 5, Ventral view of internal mould, F.5265. 6a-c, Ventral and dorsal views of internal mould, F.5262, holotype; 6c, $\times 2$. 7-8, Postero-dorsal views of internal moulds, F.5269, F.5268, $\times 2$. Both show dental lamellae, dorsal median septum, and the separation of the septum from the hinge-plate. Fig. 8 also shows the pair of thickened ridges diverging from the septum beneath the hinge-plate. 9, Internal mould of brachial valve showing weakly impressed muscle scars; destroyed by fire, $\times 2$.

Figs. 10-17. *Peruvispira kuttungensis* sp. nov. 10, 13-16, Views of several specimens destroyed by fire, all $\times 2$. Note the parietal lips in 15 and 16. 11-12, 17, F.4935A, F.4935, and F.4937. Holotype F.4935, $\times 2$.

Figs. 18-30. *Levipustula levis* Maxwell. 18-20, Exteriors of three brachial valves showing form of cardinal process and fine external spines. Note large spines from ears of pedicle valve in Fig. 18. F.4949A, F.4933A, $\times 4$ and F.4954A, $\times 2$. 21-24, Interiors of four brachial valves showing the variation in the area immediately in front of the cardinal process, and in the adductor scars. The brachial ridges in Fig. 24 are unusually well developed and the cardinal process is broken. F.4953, F.4957B, F.4952, and F.5304; all except Fig. 23 are $\times 2$. 25-26, Internal moulds of pedicle valves viewed ventrally, F.4966 and F.4963. 27, 28, 30, Views of parts of external surfaces of pedicle valves, showing spine arrangements on body of valve and on ears. F.4977D, F.4957A both $\times 2$, and Fig. 30 destroyed by fire. 29, Lateral view of internal mould of pedicle valve, F.4969.



Neerkol Series with similar surface characters but which are preserved solid and have a circular cross-section.

The species is only doubtfully referred to *Rhombopora* since there is no differentiation of the acanthopores into a single megacanthopore at the distal edge of each aperture and micracanthopores elsewhere. It may possibly be allied to *Megacanthopora* Moore.

?Rhombopora bifurcata sp. nov.

Plate 60, figs. 5–7

Holotype. F.4706C; paratypes F.5249A–E and F.4714B from beds below the main *Levipustula* bed; F.4737C–E associated with *Alispirifer* bed above main *Levipustula* bed.

Description. Narrow zoarium of short branches almost uniform in width; probably circular in transverse section though all specimens squashed; zoarial width ranges from 0.8 to 1.5 mm.; no proximal portions of zoaria observed; the largest preserved specimen c. 20 mm. long consisting of a colony twice dividing symmetrically into two equal branches similar in width to the parent; apertures situated within elongate regularly arranged rhombic depressions in the surface; rhombs outlined by rather sharp ridges formed from edge of zooecial walls; length of rhombs varies from 0.5 to 0.9 mm. (though most lie between 0.6 and 0.8 mm.) and width from 0.2 to 0.3 mm.; aperture sometimes clearly defined by a distinct break of slope, but often vestibule merges imperceptibly into inner wall; apertures vary considerably in outline, some being simply oval, a few tending to be circular, and others elongate and pointed distally but rounded proximally; apertural lengths, where measurable, vary between 0.15 and 0.25 mm., and widths between 0.07 and 0.15 mm.; acanthopores (megacanthopores) common, giving rise to stout distally directed spines, and placed one at the distal end of each rhomb making four around each aperture, or frequently two near the end of each rhomb and odd ones along the sides making up to eight around some apertures; immature portions of zooecia apparently arise from an axis, have thin walls, and appear to be irregularly depressed in outline in transverse section; as they approach maturity, zooecia increase gradually in diameter and curve rather sharply to mature region where they decrease slightly in width to the aperture; no diaphragms or hemisepta; skeletal material in mature region dense; apparently no vesicular tissue present anywhere in zoarium.

Remarks. Most of the specimens are preserved as moulds, and no material suitable for preparing thin sections has been discovered. The internal details have been observed either in the moulds or on polished surfaces of partly decomposed specimens. I know of no species with which to compare it.

Family FENESTELLIDAE King 1850

Genus FENESTELLA Lonsdale 1839

Type species *F. antiqua* Lonsdale, Silurian, England.

Fenestella cerva sp. nov.

Plate 59, figs. 1a–c

Holotype. F.4718; paratypes F.4705G–H and F.4709A, all from below the main *Levipustula* bed near 019840.

Description. Zoarium with $5\frac{1}{2}$ –6 fenestrules and ten to twelve branches in 10 mm.; branching frequent; obverse surface of branches with high sharply defined keel occupying up to almost half width of branch; apertures situated in a distinct shallow depression on either side of keel; nodes high, oval at base, spaced at intervals of 0.6–1.2 mm. and numbering twelve to eighteen per 10 mm.; whole of obverse surface, including keel, with very delicate striae on which are very fine pustules of variable strength; reverse surface of branches well rounded and finely striate; apertures exsert, surrounded by peristomes usually almost circular in outline and often slightly higher proximally than distally; apertural diameter 0.12–0.18 mm., and centres of apertures usually 0.35–0.50 mm. apart with some up to 0.60 mm.; change from two to three rows of apertures takes place immediately prior to branching; usually four to five apertures per fenestrule, rarely three; dissepiments short—0.1–0.25 mm., either slightly above or below the level of the branches on obverse surface, and delicately striate; on reverse surface dissepiments slightly depressed; junction between branches and dissepiments angular making for sub-rectangular fenestrules, though some are slightly oval; fenestrule length 1.3–2.2 mm., most being 1.5–2.0 mm., and width 0.4–0.8 mm., zooecia irregularly subpentagonal in outline on basal plate.

Remarks. This species is not unlike *F. malchi* (Crockford) in many respects, but it can be distinguished from that form by its slightly longer fenestrules, sharply defined carina, and probably also by the peristomes. The latter are not mentioned in Crockford's original description. According to the text (Crockford 1948, p. 422) *F. malchi* has four, rarely three, apertures per fenestrule, but the figure of the type shows four to five. Should the former be accurate, then this character is another basis of distinction from *F. cerva*.

Fenestella stellaris sp. nov.

Plate 58, figs. 4a–d

Holotype. F.4716A–B; paratype F.4717; both from below the main *Levipustula* bed near 019840.

Description. Rather rapidly branching; ten to twelve fenestrules and fifteen to eighteen branches in 10 mm.; obverse surface of branches broadly rounded, reverse surface much more sharply rounded; branches 0.20–0.35 mm. wide at middle of fenestrules; number of rows of apertures increases to three only 1 mm. or so prior to bifurcation; usually two, occasionally three apertures per fenestrule; apertures strongly exsert, surrounded by high peristomes, from which arise eight to nine projections which continue down inside the peristome as septum-like plates; at base of these plates, aperture crossed by

EXPLANATION OF PLATE 57

All figures are of rubber casts.

Fig. 1. *Fenestella rectangularis* (Crockford). 1a, Obverse surface, F.4709B–C, $\times 4.6$. 1b, Enlargement of same, $\times 10$. 1c, Reverse surface of same, $\times 10$. Bubbles in the rubber along the keel in 1a–b mark the position of the nodes, and in 1c the positions of small pustules shown elsewhere as slightly lighter coloured patches.

Fig. 2. ? *Fenestella altinodosa* sp. nov. 2a, Obverse surface, F.4708A, holotype, $\times 5$. The white spots on the branches mark the positions of the large nodes. 2b, Enlargement of same, $\times 9$.

Fig. 3. *Fenestella anodosa* sp. nov. 3a, Obverse surface, F.4700B–C, holotype, $\times 4.5$. 3b, Enlargement of another part of same zoarium, $\times 10$. 3c, Reverse surface of same, $\times 4.5$.



axially perforated, arched, diaphragm-like plate; diameter of apertures 0.12–0.16 mm.; centres of adjacent apertures 0.3 to 0.45 mm. apart; no median keel; large nodes directed distally and irregularly arranged on obverse surface—never in a median row; numerous subrounded depressed areas irregularly scattered over surface between apertures; apertures never open into depressed areas; fenestrules oval to subrectangular, 0.5–0.8 mm. long and 0.3–0.4 mm. wide; dissepiments 0.2–0.25 mm. long; striae on reverse surface weak or absent, but surface with large distally directed spines of irregular size and distribution, often situated on the branches at their junction with the dissepiments.

Remarks. The nodes on the obverse surface lie at an unusually low angle to the surface, and their arrangement is highly irregular. In some places they are less than 0.5 mm. apart, and elsewhere 4 or 5 mm. apart. Occasionally they occur in groups of three or four.

It differs from all other Carboniferous species in its node arrangement and in the depressed areas on its surface into which the apertures do not open.

Fenestella anodosa sp. nov.

Plate 57, figs. 3a–c

Holotype. F.4700B–C; paratype F.4701; both from above the main *Levipustula* bed near 019840.

Description. Zoarium with $4\frac{1}{2}$ – $5\frac{1}{2}$ fenestrules and about twelve branches per 10 mm.; branches normally 0.3–0.5 mm. wide, expanding to 0.9 mm. prior to bifurcation; keel of variable height, but always prominent, and in places tending to be bladed; no nodes; branches moderately furrowed on each side of keel; reverse surface broadly rounded, striate and without nodes; apertures 0.16–0.22 mm. in diameter and 0.40–0.52 mm. apart; peristomes strong; on some parts of the branches are low sharp transverse ridges joining the keel to the fenestrules; these ridges variably spaced, but as little as about 0.25 mm. apart in some areas and completely absent in others; change from two to three rows of zooecia takes place from 0.5–3.0 mm. prior to bifurcation, there being two strong keels separating the three rows of apertures; four, rarely five, apertures per fenestrule; dissepiments 0.1–0.2 mm. long, and on the general level of the branches on both the obverse and reverse surfaces; fenestrules subrectangular to suboval, 1.5–2.1 mm. long and 0.4–0.6 mm. wide; zooecia subpentagonal on the basal plate.

Remarks. The two main distinguishing features of this species are the sharp keel without nodes, and the sharp transverse ridges across the branches. These latter give a very knobbled appearance of distinctive type to the moulds. *F. cincta* (Crockford) has similar ridges on the obverse face, but these apparently always surround an aperture, whereas on *F. anodosa* they isolate depressed areas both around and between the apertures. *F. cincta* also has a very much coarser mesh.

Fenestella crockfordae sp. nov.

Plate 59, figs. 2a–b

Holotype. F.4699A–B; paratypes F.4698 and F.4697A–B; all from above the main *Levipustula* bed near 019840.

Description. Zoarium with $3\frac{1}{2}$ – $4\frac{1}{2}$ fenestrules and ten to twelve branches in 10 mm.; obverse surface of branches with high, broad, usually well-rounded keel; nodes high,

oval at base, numbering eight to eleven per 10 mm., and situated 1.0–1.5 mm. apart; strong depression along branches on either side of keel; whole obverse surface, including dissepiments with delicate striae, carrying very fine pustules; reverse surface well-rounded striate, and without nodes; apertures circular to slightly oval and surrounded by strong peristomes; apertural diameters 0.16–0.20 mm., and centres of adjacent apertures 0.35–0.55 mm. apart; many apertures covered by a centrally perforate plate at base of peristome; change from two to three rows of apertures takes place immediately before branching; four to six apertures per fenestrule; fenestrules subrectangular in shape ranging in length from 2.0–3.2 mm. (most 2.2–2.6 mm.), and in width from 0.5–0.8 mm.; zooecia irregularly subpentagonal on the basal plate.

Remarks. The mesh structure clearly separates this species from all others so far described from the Australian Carboniferous.

Fenestella stroudensis sp. nov.

Plate 56, figs. 1a–c

Holotype. F.4704A–B; paratype F.4703, both from below the main *Levipustula* bed near 019840.

Description. Zoarium with $5\frac{1}{2}$ fenestrules and ten to twelve branches in 10 mm.; obverse surface with weak, blunt keel, and sometimes keel virtually absent; no nodes; no furrow developed lateral to keel; whole surface with strong wavy striae; reverse surface of branches broadly rounded, strongly striate, and without nodes; apertures circular to slightly oval, 0.16–0.20 mm. in diameter, and with their centres 0.30–0.50 mm. apart; peristomes thin and moderately high; change from two to three rows of apertures up to 3 mm. prior to bifurcation; usually four, rarely five, apertures per fenestrule; dissepiments 0.12–0.16 mm. long, generally more or less on a level with the branches on the obverse surface, slightly raised or slightly depressed on the reverse; fenestrules subrectangular to suboval; fenestrules 1.5–2.0 mm. long and 0.4–0.8 mm. wide, occasional ones wider.

Remarks. The low keel and the absence of nodes separates this species from other members of the fauna with similar mesh dimensions.

? *Fenestella altinodosa* sp. nov.

Plate 57, figs. 2a–b

Holotype. F.4708A, from the Booral Formation, below the main *Levipustula* bed near 019840.

Description. Rather coarse mesh, with six to seven fenestrules and about twelve branches in 10 mm.; fenestrules 1.3–1.8 mm. long and 0.4–0.6 mm. wide; branches 0.4–0.5 mm.

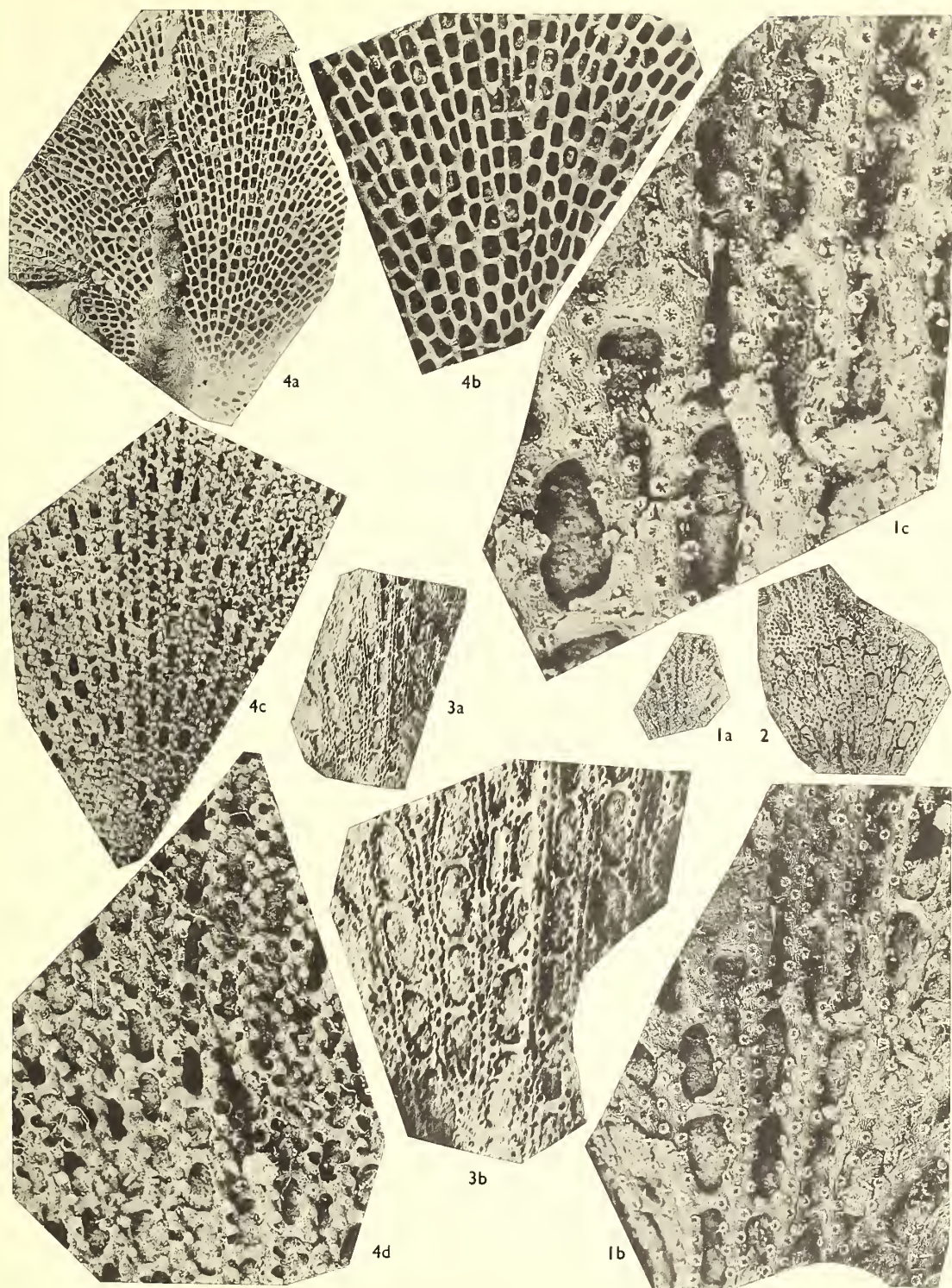
EXPLANATION OF PLATE 58

All figures of rubber casts except Fig. 2.

Figs. 1–2. *Polypora septata* sp. nov. 1a–c, Obverse surface of holotype, F.4708D, $\times 1.5$, 10, and 20 respectively. 2, Mould of obverse surface of F.4734D, $\times 2.5$.

Fig. 3. *Polypora* sp. 3a–b, Obverse surface of specimen destroyed by fire, $\times 1.9$ and 5 approximately.

Fig. 4. *Fenestella stellaris* sp. nov. 4a–b, Reverse surface of holotype, F.4716A–B, $\times 2$ and 4. Note numerous rounded nodes. 4c–d, Obverse surface of same, $\times 4.7$ and 10.5. Note large depressions in surface of branch between apertures.



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wide, expanding to 1.0 mm. prior to bifurcation; edges of branches on obverse face forming a sharp rim to the fenestrules; surface of branches with strong raised ridges usually six in number, but increasing to twelve prior to bifurcation; sometimes median ridge slightly stronger than those on either side; ridges very finely pustulose; dissepiments arched, raised well above the general level of the surface of the branches and carrying lateral extensions of the ridges from the branches; nodes very large, circular to slightly oval at the base where the diameter is 0.12–0.20 mm., and fluted; nodes somewhat irregularly spaced at nine to fifteen per 10 mm., and not always situated along the mid-line; apertures with strong peristomes, slightly oval in outline and 0.20–0.24 mm. in longitudinal diameter; increase from two to three rows of apertures takes place from 2–4 mm. prior to branching; distance between successive apertures is 0.40–0.50 mm.; usually four, occasionally three apertures per fenestrule.

Remarks. The high nodes clearly distinguish this species. There is no trace of a mesh-work such as that characteristic of *Hemitrypa*, and so far as can be determined at present the nodes terminate bluntly. However, the possibility that there are expanded terminations to the nodes in places has not been ruled out.

Other odd features of the species are the absence of a clearly defined median carina, the development of the nodes from any part of the obverse surface, and the increase from two to three rows of apertures on the branches well before bifurcation. Perhaps it would be equally well placed in *Polypora*.

Fenestella rectangularis (Crockford)

Plate 57, figs. 1a–c

1948 *Fenestrellina rectangularis* Crockford, p. 425, fig. 7.

Material. F.4705D–F, F.4709B–C, all from the Booral Formation, below the main *Levipustula* bed, near 019840.

Remarks. This species has not previously been recorded from New South Wales, though it is common in Queensland. The specimens agree very well with the original description, but their range of variation is slightly wider in some characters. The fenestrules are 0.9–1.4 mm. long; the apertures 0.1–0.18 mm. in diameter; the nodes 0.6–0.9 mm. apart, and they number fourteen to eighteen per mm. Features not previously noted are the presence of numerous nodes of irregular size and spacing on the reverse surface; the presence of a shallow furrow in which the apertures are situated, on either side of the keel; the keel is variable in height and width, but is always well rounded, and the nodes vary in size to a remarkable degree even on the one individual; the whole of the obverse face including the keel is very delicately striate and pustulose; the zooecia are sub-pentagonal on the basal plate, but are also inclined to be pointed proximally to the inclination of the cells to the line of the branches; the change from two to three rows of zooecia takes place immediately prior to branching.

Fenestella sp. cf. *rectangularis* (Crockford)

Material. F.4738A–D, F.4740A–B, F.4741A–B, F.4743A–B, all from the Isaacs Formation near 987823.

Remarks. This species has similar mesh dimensions, zooecial and node spacing, and keel structure to *F. rectangularis*, but differs in having no nodes on the reverse surface of the

branches, and in the development of a double keel and three rows of zooecia on the branches up to 0.5 mm. prior to bifurcation.

Fenestella malchi (Crockford)

1948 *Fenestrellina malchi* Crockford, p. 422, fig. 4.

Material. F.4739 from the Isaacs Formation near 987823.

Remarks. This specimen shows all of the characters of this species except that the nodes are slightly closer together than normal.

Fenestella cf. *cincta* (Crockford)

Material. F.4697C, F.4700A, F.4715E, F.4719, F.4726C-D, from the Booral Formation above the main *Levipustula* bed near 019840.

Remarks. These specimens have the dimensions and fenestrule shape of the types. The keel, however, is very variable in height, being broad and rounded to rather high and sharp though it is never clearly defined. The edges of the branches are sometimes slightly raised and sharp, so that the zone occupied by the apertures on either side of the keel is slightly excavate. Other points of distinction from the types are the slight raising of the dissepiments above the general level of the branches on both surfaces, and the infrequency with which the depressed areas bounded by thin sharp ridges occur on the obverse face.

A feature not previously observed is that no increase from two to three rows of zooecia takes place prior to bifurcation of the branches.

Fenestella osbornei (Crockford)

Plate 59, fig. 3

1948 *Fenestrellina osbornei* Crockford, p. 424, fig. 5.

Material. Numerous specimens from throughout the fossiliferous section except for the *Liriplica* bed, near 019840.

Remarks. This is the most common species of *Fenestella* in the fauna. Its type locality is in the Booral Formation near where the bulk of the present collection has been obtained. Its variability is much greater than indicated by Crockford, and apparently it is one of the species in which the mesh structure changes during the growth of the colony. On one individual, fenestrule length changes from 0.55–0.7 mm. at the early

EXPLANATION OF PLATE 59

All figures except Fig. 4 are of rubber casts.

Fig. 1. *Fenestella cerva* sp. nov. 1a, Part of the obverse surface of F.4718, holotype, $\times 2$. 1b–c, Part of surface of same, $\times 8$.

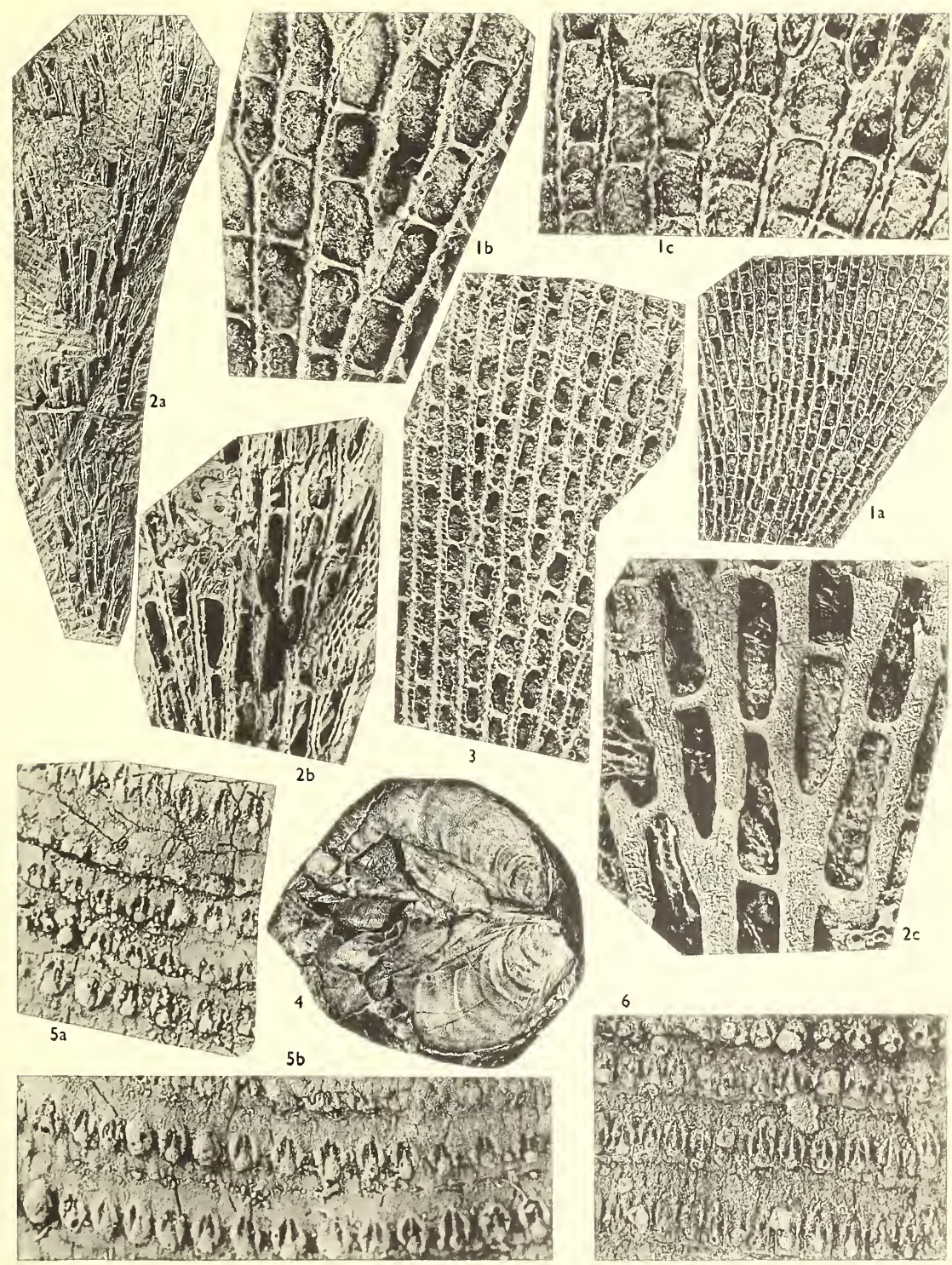
Fig. 2. *Fenestella crockfordae* sp. nov. 2a, Obverse surface of F.4699A–B, holotype, $\times 2$. 2b, Part of surface of same, $\times 4$. 2c, Reverse surface of same, $\times 10$. Note fragment of *R. bifurcata* in 2a–b.

Fig. 3. *Fenestella osbornei* (Crockford). Part of obverse surface of well-preserved specimen, F.4702, $\times 7$ approximately.

Fig. 4. *Posidonia* sp. Internal mould of badly crushed specimen, F.4039, $\times 1$.

Fig. 5. *Phricodothyris immensa* sp. nov. 5a–b, Detail of spine bases, F.4914G and F.4916A, $\times 12$.

Fig. 6. *Phricodothyris booralensis* Campbell. Detail of spine bases, F.4902B, $\times 12$.



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stages to 1.0–1.2 mm. at the later, with a consequent reduction from fourteen to nine fenestrules per 10 mm., and a change from two to three apertures per fenestrule. Only rarely are there four apertures per fenestrule, though according to the figure of the holotype this is common. The keel though sometimes weak is always distinct, and is variable in both width and height. The dissepiments are not always depressed below the level of the branches on the obverse surface, and indeed there are some specimens in which they are almost all on a level with, or slightly above, the branches. There are no nodes on the reverse surface, and the zooecia are subpentagonal to triangular in outline on the basal plate.

Fenestella micropora (Crockford)

Plate 63, figs. 2a–c

1948 *Fenestrellina micropora* Crockford, p. 424, fig. 3.

Material. F.4741C–D, F.4742A–B, F.4743C–D and numerous small fragments, all from the Isaacs Formation near 987823.

Remarks. My specimens of this species agree almost completely with the description and dimensions of the types. One minor difference is in the lengths of the fenestrules and dissepiments, the former being slightly shorter (0.4–0.45 mm.) and the latter slightly longer (0.06–0.08 mm.) than in the types. Other features not previously noted are the sharp edging of all the branches on the obverse surface, the not infrequent arching of the dissepiments to the level of the top of the carina, and the subpentagonal to triangular outline of the zooecia on the basal plate.

Genus POLYPORA M'Coy 1844

Type species *P. dendroides* M'Coy, Lower Carboniferous, Ireland.

Polypora scalpta sp. nov.

Plate 60, fig. 11

Holotype. F.4720A–B, Booral Formation, above main *Levipustula* bed near 019840.

Description. Six to seven fenestrules and eight to ten branches in 10 mm.; branches c. 0.7 mm. wide, increasing to 1.1–1.3 mm. prior to bifurcation; fenestrules 0.8–1.2 mm. long and 0.2–1.4 mm. wide; branches flattened on obverse face and carrying four rows of apertures, increasing to five just prior to and decreasing to three after bifurcation; rows of apertures well defined and separated by well-marked sinuous ridges; each aperture slightly sunken, but with a narrow sharp peristome; apertures circular to slightly oval in outline, and with a longitudinal diameter of 0.20–0.25 mm.; two to three apertures per fenestrule; centres of adjacent apertures 0.40–0.50 mm. apart; dissepiments 0.3–1.1 mm. long (most being between 0.5 and 0.8 mm.) and with their surfaces on more or less the same level as the branches; no nodes present; zooecia broadly flattened on basal plate and irregularly polygonal in outline; branches markedly flattened—about 0.30 mm. thick where measurable; reverse surface with very weak striae, and carrying minute pustules.

Remarks. *P. pustulosa* has smaller, more closely spaced apertures which are raised rather than depressed, and which are pustulose around the peristome. There are also minor

differences in mesh dimensions. *P. neerkolensis* is comparable in overall dimensions and in the large size of the apertures, but it has longer fenestrules, shorter dissepiments, more zooecia per fenestrule, and somewhat narrower branches.

The Permian *P. pertinax* Laseron, from the Allandale Formation of New South Wales, is comparable in size and zooecial count, but differs in the smaller size of its apertures and its shorter dissepiments.

Polypora septata sp. nov.

Plate 58, figs. 1-2

Holotype. F.4708D from below the main *Levipustula* bed: paratypes F.4715C-D and F.4734C-D from above and below the main *Levipustula* bed respectively; near 019840.

Description. Zoarium with 5-6½ fenestrules and nine to thirteen branches per 10 mm.; obverse surface of branches broadly rounded and carrying twenty to thirty slightly wavy striae along which are rows of pustules; branches 0.3-0.5 mm. wide where three rows of apertures; reverse surface of branches broadly rounded, delicately striate and with delicate pustules twenty to twenty-five per mm. along the striae; branching frequent; apertures strongly exsert, surrounded by high sharp peristomes; apertures arranged in three rows, but increasing to four up to 2 mm. prior to, and decreasing to two up to 2 mm. subsequent to bifurcation; apertures circular and 0.12-0.16 mm. in diameter; centres of adjacent apertures 0.30-0.50 mm. apart; aperture at base of peristome crossed by a centrally perforated plate from which arise eight to ten septum-like plates; when well developed these plates reach almost to the axis of the aperture leaving a narrow central tube, and imparting a markedly stellate appearance; no apertural spines observed; three to four apertures per fenestrule and four to five per fenestrule and dissepiment; dissepiments short, normally 0.1-0.3 mm. long, but occasional ones reach 0.6 mm.; on the reverse surface dissepiments on the general level of the branches, but on the obverse surface slightly depressed; fenestrules oval to subrectangular, 1.1-1.8 mm. long and 0.3-0.7 mm. wide; zooecia more or less rhombic in outline on basal plate.

Remarks. This species differs from *P. tenuirama* Crockford in its smaller fenestrules and the smaller number of zooecia per fenestrule. *P. tenuirama* is said to have 'about nine tiny radiating spines around each aperture', but no mention is made either of a centrally perforated diaphragm-like plate or of septa within the peristome. It is possible that the

EXPLANATION OF PLATE 60

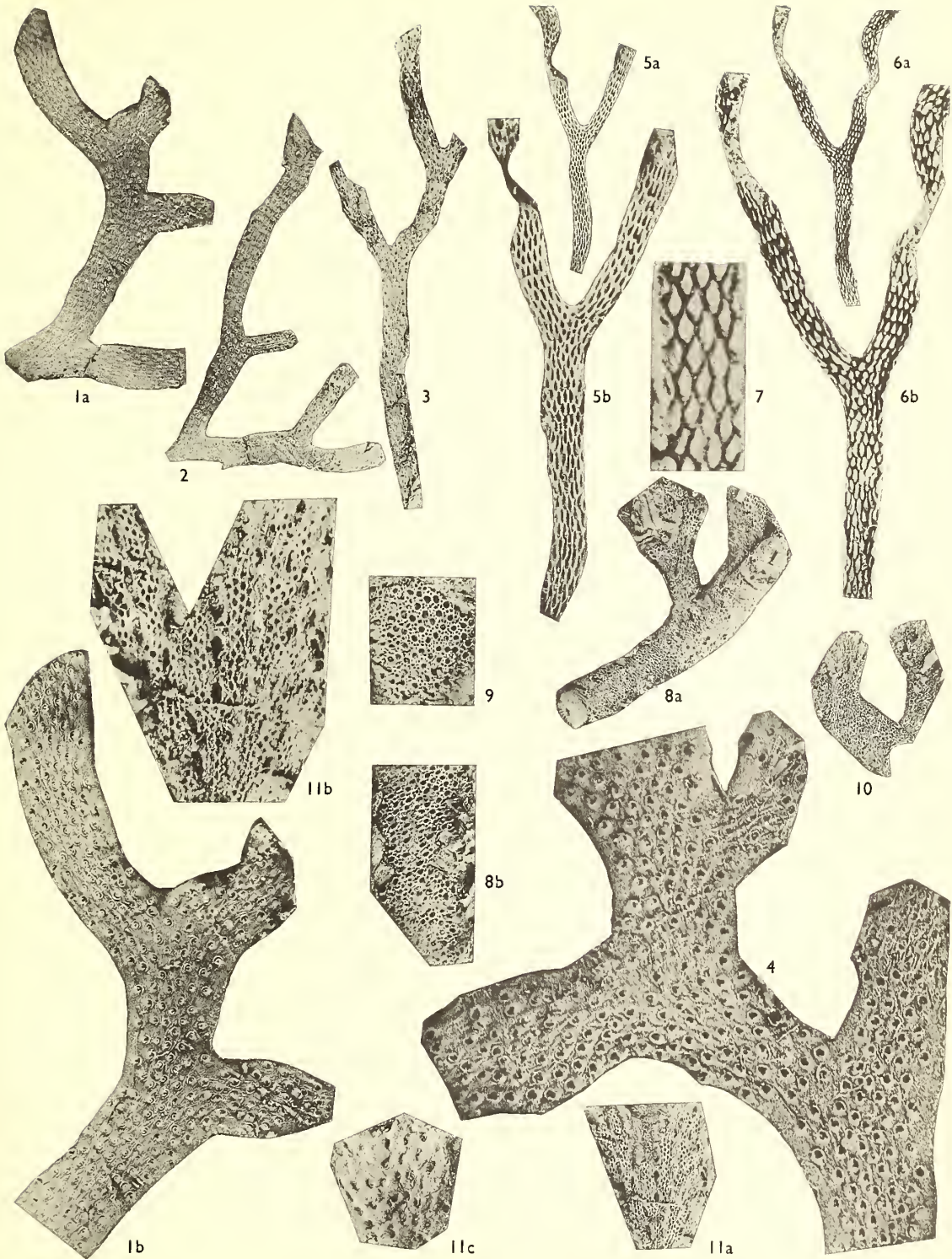
All photographs are of rubber casts unless otherwise stated.

Figs. 1-4. *Fistulina frondescens* Crockford. 1a-b, Surface of F.4705i, ×2 and 4 respectively. 2, F.4705c, ×2. 3, F.4706a, ×2. 4, F.4728, ×6. Note the differently shaped apertures and lunaria in 1b and 4.

Figs. 5-6. ? *Rhombopora bifurcata* sp. nov. 5a-b, Rubber cast of F.4706c, holotype, ×2 and 4.5 respectively. 6a, b, Original mould of F.4706c, ×2 and 5 respectively. 7, Mould of part of the surface of F.5249a, ×12. Note the pits left by the acanthopore spines.

Figs. 8-10. ? *Stenocladia enigma* sp. nov. 8a, F.4720b, ×2, holotype, showing encrustation on a crinoid stem with two laminar expansions. 8b, Part of surface of same, ×4. 9, F.4721, ×4, small fragment showing arrangement of mesopores. 10, F.4720c, ×2, laminar expansion.

Fig. 11. *Polypora scalpta* sp. nov. 11a, Obverse surface of holotype, F.4720a-b, ×2. 11b, Reverse surface of same, ×5. 11c, Obverse surface of same, ×2.



latter structures have been described as spines. The similarity in general form, and the size and stellate nature of the apertures, is so great that were it not for the constancy of the Booral specimens in fenestrule size and zooecial count, I would have had no hesitation in placing them in *P. tenuirama*.

Polypora sp.

Plate 58, figs. 3a-b

Material. Several specimens since destroyed by fire.

Description. Zoarium with $3\frac{1}{2}$ – $4\frac{1}{2}$ fenestrules and seven to eight branches per 10 mm.; branches 0.45–0.8 mm. wide where there are three rows of apertures, but expand to 1.0–1.3 before bifurcation; obverse surface of branches broadly flattened or even slightly concave; three rows of zooecia increasing to four up to 4 mm. prior to, and decreasing to two up to 2 mm. subsequent to bifurcation; rows of apertures clearly defined and in some places separated by low rounded ridges; edges of branches along fenestrules sharp and frequently raised into narrow keel-like ridges; two, or occasionally three, faint flexuous striae between neighbouring rows of apertures, bending out around apertures and in again; no nodes; apertures slightly oval in outline, and 0.15–0.24 mm. long; peristomes broad and low; centres of adjacent apertures 0.4–0.55 mm. apart; four to five apertures, occasionally six, per fenestrule; dissepiments 0.15–0.3 mm. long, slightly raised above, or on the same level as the branches on the obverse surface, and slightly depressed on the reverse; fenestrules oval to subrectangular, 1.9–2.6 mm. long and 0.3–0.9 mm. wide; zooecial cells long, *c.* 0.8–1.0 mm. long from the distal edge of the aperture to the inner tip, more or less tubular, but tapering to a blunt point.

Remarks. The nearest described species is *P. neerkolensis* from the Neerkol Series at Rockhampton and Mt. Barney, Queensland. However, that form has fewer apertures per fenestrule, the fenestrules are smaller, and there do not appear to be any broad ridges between the rows of apertures, though the fine surface striae are present.

Polypora isaacsensis sp. nov.

Plate 63, figs. 1a-e

Holotype. F.4744A-C, from the Isaacs Formation near 987823.

Description. Zoarium with eleven to twelve fenestrules and fourteen to sixteen branches in 10 mm.; branching frequent; branches flattened to broadly rounded on obverse surface; and strongly rounded on reverse surface; apertures usually in three rows, increasing to five a short distance before branching; two to three apertures to a fenestrule; distance between centres of successive apertures 0.32–0.36 mm.; apertures well rounded to oval in outline, exsert, with distinct sharp peristomes, and 0.12–0.16 mm. in diameter; eight to ten narrow septum-like partitions divide the aperture within the peristome, and extend less than one-quarter of the way across the aperture; plate with median perforation crosses aperture at base of partitions; numerous well-rounded depressions irregularly arranged on surface of branches between apertures; depressions usually *c.* 0.25 mm. in diameter; fenestrules oval in outline, 0.60–0.80 mm. long and 0.30–0.50 mm. wide; dissepiments 0.2–0.3 mm. long; dissepiments on level with or depressed slightly below the surfaces of the branches on both the obverse and reverse

faces; reverse surface apparently without striae, but with strong spines of variable size, irregularly arranged, but numbering eight to fourteen per 5 mm. longitudinally; internally zooecia very thick walled; bases of zooecia well rounded and oval in outline on the basal plate.

Remarks. The depressions on the obverse faces of the branches are very variably distributed. On some parts of the zoarium they are almost as abundant as the zooecia, but elsewhere there are none at all on some branches for distances of 1 cm. or more. The perforated diaphragm-like plate across the aperture inside the peristome has not been observed in all individuals, but this is probably due to poor preservation. On the reverse surface the spines are generally in an irregular row towards the middle of the branch, but in places there are pairs side by side, and especially where the branches widen before branching there are often clusters of four or five.

From *P. septata* and *P. tenuirama*, both of which are similar in the possession of septum-like plates inside the peristome (see comments on *P. septata*), *P. isaacensis* is readily distinguished by the depressions on the surface of its branches, and by its much finer mesh.

Order CYCLOSTOMATA Busk 1852
Family HEXAGONELLIDAE Crockford 1947
Genus FISTULAMINA Crockford 1947

Type species *F. inornata* Crockford, Lower Carboniferous, New South Wales.

Fistulammina frondescens Crockford

Plate 60, figs. 1-4

1948 *Fistulammina frondescens* Crockford, p. 420, figs. 1-2.

Material. Numerous specimens from throughout the whole fossiliferous section near 019840.

Remarks. The types of this species were collected from the Booral Formation, probably close to the locality where most of the present specimens have been obtained.

To date, all of the species described have been diagnosed on the basis of the width of the branches, the branching pattern, the number of rows of zooecia, the spacing of the zooecia, the size of the apertures, and the development of peristomes and lunaria. All

EXPLANATION OF PLATE 61

All figures natural size, and of rubber casts unless otherwise stated.

Fig. 1. *Calloconularia minima* sp. nov. Several specimens exposed on a slab, F.4123, with large specimen in centre as holotype, $\times 2$.

Figs. 2-5. *Limipecten pincombei* (Mitchell). 2, External mould of part of left valve, destroyed by fire. 3, Interior of left valve, F.26457 Aust. Mus. Coll., lectotype. 4, Exterior of part of left valve, F.25577 Aust. Mus. Coll. 5, Interior of right valve, destroyed by fire.

Figs. 6-7. *Cypricardinia* sp. 6, Interior of right valve, F.4921, $\times 2$. 7, Exterior of left valve, destroyed by fire. The depression below the posterior socket is an irregularity developed during fossilization.

Fig. 8. *Sanguinolites* sp. Incomplete internal mould of parts of both valves, F.4546.

Figs. 9-16. *Limipecten flexiauriculus* sp. nov. 9, 14, Umbonal parts of two right valves, F.4870 and F.4878. 10, Almost complete right valve, destroyed by fire. 11, Interior of left valve, F.4867, holotype. 12, Exterior of right valve, F.4868A. 13, Exterior of left valve, destroyed by fire. 15-16, Exteriors of parts of left valves, F.4883A and F.4871.



these features have been found to be highly variable in the present collection. The following description supplements the original. Branch width 1.5–4.5 mm. without break in range; branching at regular or irregular intervals; in some individuals branching occurs every 5–7 mm. while others run for 3 cm. and then branch every 10 mm. or so; no definite relation observed between branching pattern and position in zoarium, though probable that early parts branch less frequently than later; seven to thirteen rows of apertures on each branch; in each row apertures 0.6–1.4 mm. apart with wide variation within a single zoarium; peristome always raised and often produced into a marked lunarium on outer proximal sides of apertures; radius of curvature of lunaria varies from equality with that of aperture to one-half that value; length of lunaria up to two-thirds length of aperture; length of apertures 0.24–0.32 mm. though some on edges of branches up to 0.36 mm.; width of apertures 0.24–0.36 mm.; sinuous ridges on surface between apertures, and occasionally rows of apertures delineated by ridges slightly stronger than others; moulds show immature part of zooecia running parallel with mesial lamina for *c.* 2.0 mm. and short mature portion almost at 90° to zoarial surface; no vesicular tissue observed along mesial lamina, possibly as result of poor preservation.

Order TREPOSTOMATA Ulrich 1882

Family STENOPORIDAE Waagen and Wentsel 1886

Genus STENOCLADIA Girty 1911

Type species *S. frondosa* Girty, Chester Series (Mississippian), North America.

Remarks. Elias (1957) has reviewed this genus, and has referred a species of apparently similar habit to *S. ? enigma* n.sp., to it. Unfortunately the characters of the type species are not well known, and hence encrusting forms which develop bifoliate branches in the manner of the above species can be referred to the genus only tentatively.

Stenocladia ? enigma sp. nov.

Plate 60, figs. 8–10

Holotype. F.4720C–E; paratypes F.4721–F.4725; all form above the main *Levipustula* bed near 019840.

Description. Zoarium encrusting or forming flattened or almost cylindrical bifoliate branches; where encrusting, zoarium 0.4–0.8 mm. thick; branches of very variable thickness and width; apertures irregularly arranged, circular to strongly oval in outline and from 0.15–0.30 mm. in maximum diameter; centres of adjacent apertures 0.3–0.5 mm. apart; mesopores abundant and in one or two rows around the apertures; diameter of mesopores 0.04–0.18 mm., but most 0.06–0.08 mm.; acanthopores apparently not developed throughout the colony, but where present are large and number four or five around each aperture; no monticules or maculae; both zooecia and mesopores without diaphragms and cystiphagms; where zooecium encrusting, zooecia arise at right angles or at a high angle to the basal plate and maintain a more or less uniform diameter throughout, and mesopores extend through whole thickness of zoarium; where zoarium bifoliate, zooecia have a long immature section and a short mature section, the junction between the two sections being abrupt and angular where the zooecium is flattened but gradual and curved where it is cylindrical; no monilae.

Remarks. One of these specimens is encrusting a crinoid stem, and is at least 25 mm. long

and probably much more. From the unilaminar encrustation bifoliate extensions are developed, these varying considerably in size and shape. Another specimen apparently consists of an independent unilaminar portion giving rise to bifoliate branches. It is assumed that the former parts must have encrusted some material such as seaweed which has decomposed leaving no trace. The material is all too badly preserved to be sectioned.

Class LAMELLIBRANCHIA Blainville
Family AVICULOPECTINIDAE Eth. Jr. emend. Newell 1937
Genus LIMIPecten Girty 1904

Type species *Limipecten texanus* Girty, Lower Cisco Group, Upper Pennsylvanian, Texas.

Remarks. This genus is here interpreted in the sense of Newell (1937) who gives the generic range as Lower Carboniferous to Permian. He gives a list of six British Lower Carboniferous species which he refers to *Limipecten*. A further Lower Carboniferous species *L. newelli* from the Ardmore basin of Oklahoma was referred to the genus by Elias (1957) but its right valve is unknown and the ornament of its left valve is different from that of typical *Limipecten*.

By Pennsylvanian times the genus was well established and widespread occurring in Britain (Ramsbottom 1952), Holland (Dorsman 1945), Russia (Fedotov 1932), North America (Newell 1937), South America (Chronic 1953), China (Chao 1927), and Australia. It is also very widespread in the Permian.

Limipecten flexiauriculus sp. nov.

Plate 61, figs. 9-16

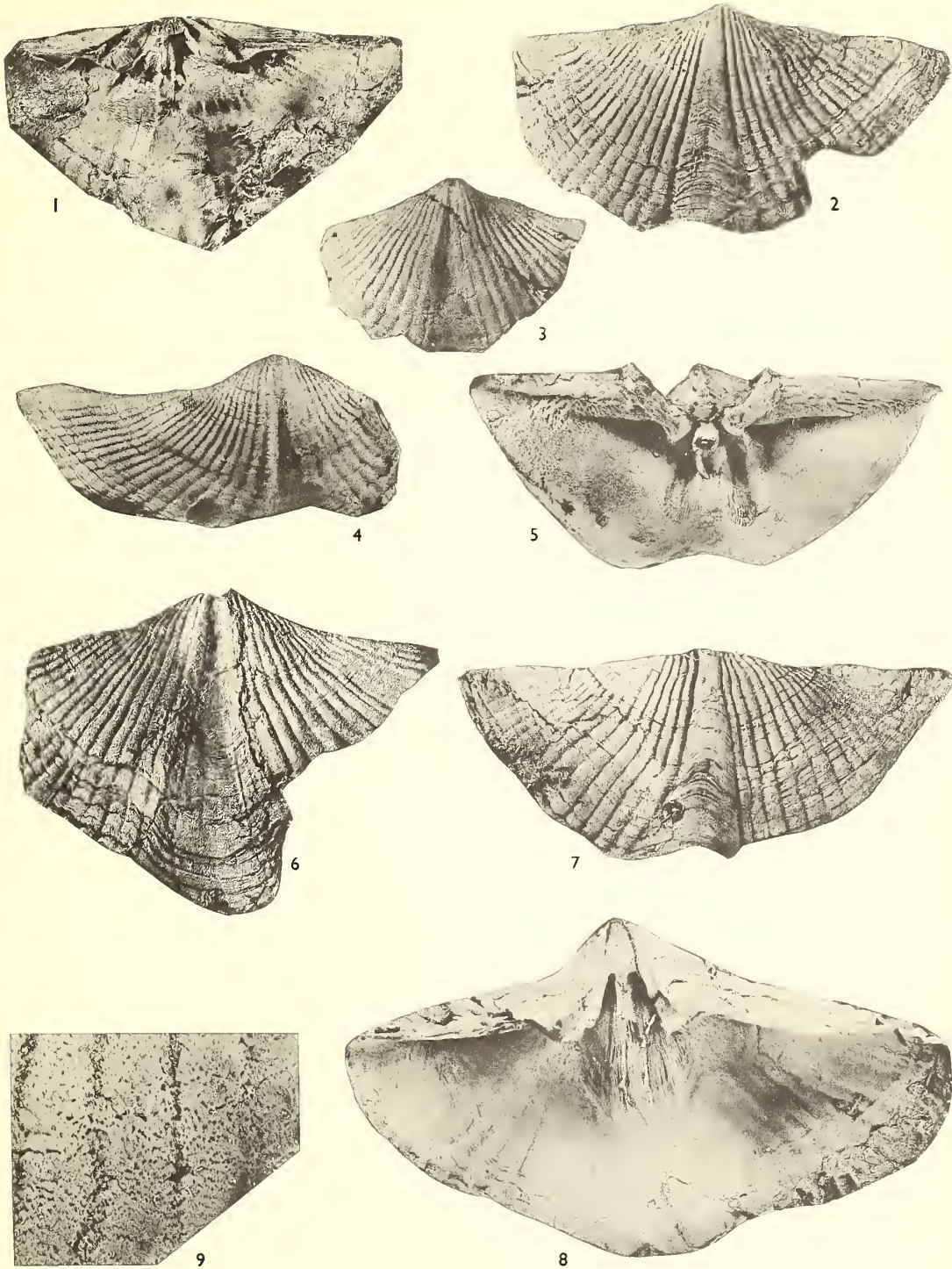
Holotype. F.4867; paratypes F.4868-F.4883, from the Booral Formation, below the main *Levipustula* bed, near 019840.

Description. Shell of moderate size for genus; neither valve markedly convex, but the left more strongly so than the right; very slightly procline to acline; hinge varies between one-half and two-thirds of the total shell length.

Left valve gently convex; anterior fold strong, slightly concave to almost straight in outline, sharply angular in section and slightly overhangs the auricle; no distinct posterior fold, but the inner edge of the posterior auricle is almost straight; umbonal angle *c.* 100°; up to forty-five robust plicae on body of valve; plicae increase by intercalation, most being emplaced within 5 mm. of the umbo, but occasional ones appear up to 30 mm.; primary plicae retain their greater size to the shell margin, and

EXPLANATION OF PLATE 62

All figures natural size unless otherwise stated, and all photographs are of rubber casts. Figs. 1-9. *Syringothyris bifida* sp. nov. 1, Interior of brachial valve, F.4915G. 2, 7, Exteriors of brachial valves, F.4914A and F.4915F. 3, 4, Exteriors of fragments of pedicle valves, F.4759 and F.4914D. 5, Interior of pedicle valve, F.4909A, showing syrxinx. 6, Exterior of pedicle valve, F.6040. 8, Interior of pedicle valve, F.4917A, holotype, showing syrxinx. 9, Detail of surface ornament, F.4912, $\times 5$.



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tend to be flatly rounded; interspaces much narrower than primary plicae; occasionally plicae bear traces of extremely fine radial striae spaced at three to five per mm. near the venter; well developed, rather evenly spaced imbricating lamellae cover the body of the valve, and vary in number from seven to eight per 3 mm. near the umbo, to three to five per 3 mm. near the anterior margin; near the umbo, lamellae run straight across costae and interspaces, but towards the middle of the valve they swing forward in the interspaces as rounded lobes, and on the adult portions tend to produce angular projections in the interspaces; well-preserved specimens show lamellae overlapping adjacent ones by up to 1 mm.; on the anterior auricles well-developed overlapping lamellae swing outward from the anterior fold but are reflexed toward the hinge-line, imparting a distinctive shape to the auricle; up to thirteen extremely weak costae on auricle; as distinct from those on the body of the valve, lamellae swing out over the costae and back in over the interspaces, or cross both costae and interspaces without change in direction; posterior auricle differentiated by a slight to strong change in slope, but at its margin there is a sudden break in the development of the plicae and the lamellae are sharply deflected dorsally; extremity of auricle rectangular, and its surface has five or six irregular rudimentary costae; lamellae strong and deflected away from the umbo where they cross the costae; ligament area almost flat, lying at an angle of less than 20° to the plane of junction of the valves, and bearing growth-lines parallel with the hinge, but no ligament grooves; resilifer broad, very shallow and very vaguely outlined.

Anterior fold of *right valve* small, slightly concave and angular, extending into a deep, steep-sided auricular sulcus; posterior fold almost straight and also small and angular; umbonal angle *c.* 100° – 110° ; ornamentation near the umbo represented by almost indiscernible traces of plicae and lamellae; approximately fifty plicae on body of valve, increasing by intercalation; plicae weaker and flatter than those of the left valve; interspaces much narrower than plicae; strength of plicae decreases and their breadth increases markedly on posterior third of the valve; closely spaced (10–12 per 5 mm.) delicate lamellae cover whole valve except umbonal region; in general, lamellae cut straight across plicae, but on more adult portions of valve they frequently move ventrad slightly in the interspaces; anterior auricle large, costate, distinctly convex, and its extremity almost semicircular; its surface with six or seven strong costae, all save the most dorsal and the most ventral originating at the umbo; lamellae very strong and produce scale-like projections where they cross the costae; posterior auricle small, sub-triangular, flattened, its extremity almost a right angle; a few weak irregular costae on its ventral half, but its dorsal half apparently non-costate; lamellae slightly stronger than those on the body of the valve and deflected distally as they cross the costae, forming small projections.

No trace of muscle scars in either valve.

Dimensions (in mm.).

Left valves

<i>Length</i>	<i>Height</i>	<i>Length of anterior auricle</i>	<i>Length of posterior auricle</i>
59	59	18	12
<i>c.</i> 50	50	14	8

Remarks. No shelly specimens have been found, but since the plicae are usually reflected on the internal moulds, it is probable that the shell was much thinner than in most American and British species of the genus.

Mitchell (1924) described eleven new pectenoid species (all of which he referred to *Aviculopecten*) from the shore of Lake Boolambayt. All of his specimens apparently came from one or two localities near Bombah Point, from which a rich *Levipustula* fauna, comparable with that from Booral, has been recovered. The material is in general rather poor, and some of it is distorted. Many of the species are based on only one or two specimens, which in my opinion are not interpretable. Further, several species are known from only the left valve, and the association of left and right valves is, as Mitchell himself noted, open to doubt.

I have examined Mitchell's complete collection, and have made a small collection of my own. From these specimens it is clear that only two species are readily recognizable, and that many are synonyms. For the two definite species the names *A. pincombei* and *A. flexicostatus* appear to be the best ones to preserve, since the syntypes of both are in a good state of preservation and there is no doubt as to their identification. *A. pincombei* clearly belongs to the genus *Limipecten* as here interpreted. The fine plication and the weak ventral projection of the lamellae in the intercostal spaces on the left valve suggest that *A. flexicostatus* should be left in *Aviculopecten*. However, the costae of the right valve appear to increase by intercalation and not by bifurcation as in that genus and so I refer it to *Limipecten* also. I here select the specimen F.26457 Aust. Mus. Coll. figured by Mitchell 1924, pl. 52, fig. 19, as lectotype of *L. pincombei*, and F.26462 Aust. Mus. Coll. figured by Mitchell 1924, pl. 51, fig. 15, as lectotype of *L. flexicostatus*.

In synonymy with *L. pincombei* is *A. andrewsi*; and with *L. flexicostatus* are *A. pyriformis*, *A. spartens*, *A. perobliquatus*, *A. argutus*, and *A. articulatus*. Some species cannot be satisfactorily interpreted on the material available. These are *A. fusiformis*, which could be merely a laterally distorted *A. flexicostatus*; *A. leggei* which is represented by only one poorly preserved individual; and *A. plicatilis* which is also based on a single juvenile specimen.

L. pincombei differs from *L. flexiauriculus* sp. nov. in the coarse costation of its left valve, the acutely triangular form of the posterior auricle, and the wing-like form of the anterior auricle. *L. flexicostatus* is clearly distinguished from both the above forms by its much finer costation, weak lamellation, and the shape of the valves.

L. flexiauriculus sp. nov. can be readily distinguished from all the described Pennsylv-

EXPLANATION OF PLATE 63

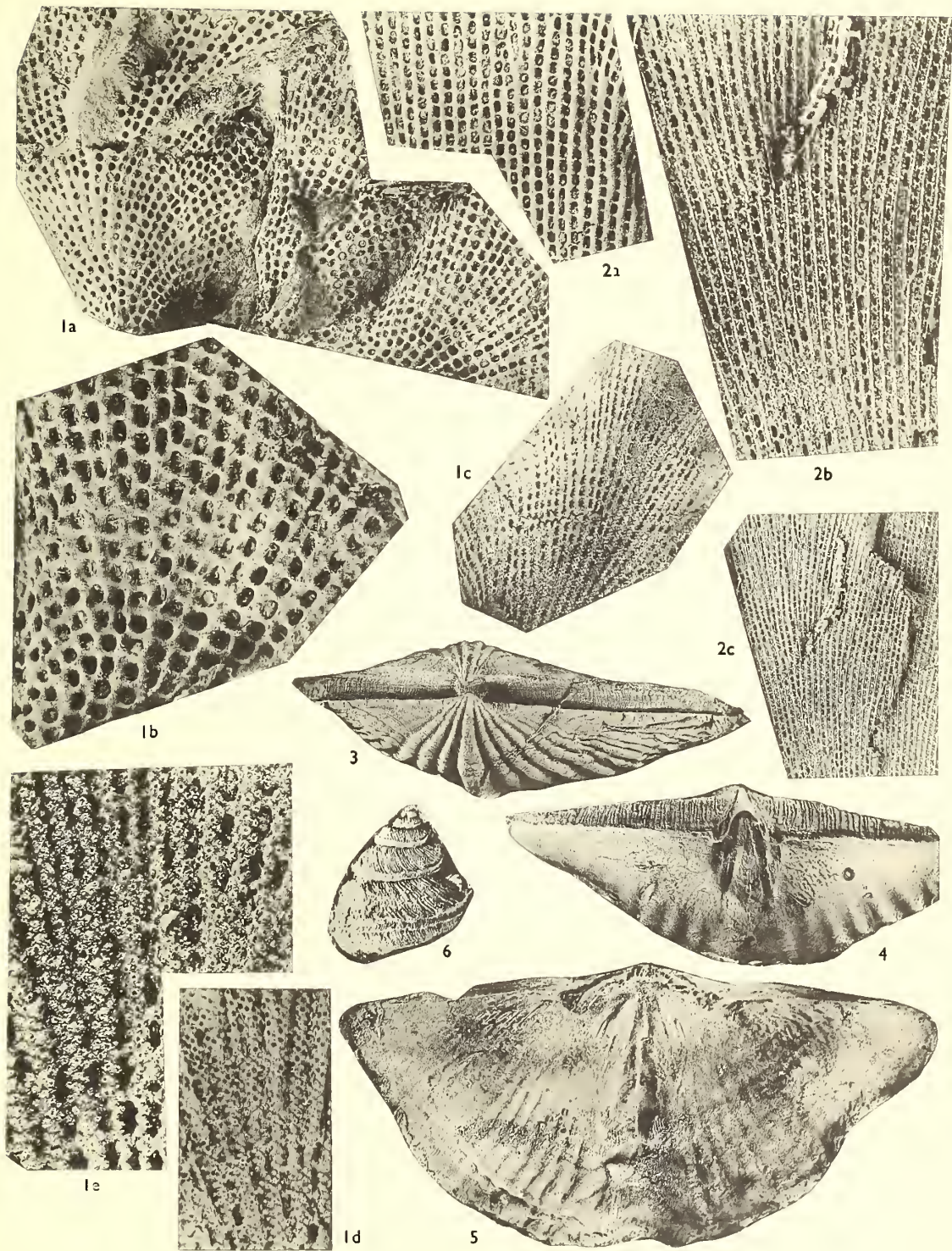
All figures are of rubber casts, and are natural size unless otherwise stated.

Fig. 1. *Polypora isaacsensis* sp. nov. 1a, Reverse surface F.4744A-B, holotype, $\times 2$. 1b, Same, $\times 4$. 1c, Obverse face of same, $\times 2$. 1d, Same, $\times 4$, showing depressions in surface of branches between apertures. 1e, Same, $\times 8$ approximately, showing arrangement of apertures.

Fig. 2. *Fenestella micropora* (Crockford). 2a, Reverse surface, F.4742A-B, $\times 4$. 2b, Obverse surface of same, $\times 4$. Bubbles in rubber along keel in lower part of figure mark position of nodes. 2c, Same, $\times 2$. Figs. 3-4. *Alispirifer laminosus undatus* subsp. nov. 3, Part of a distorted specimen, F.4759B. 4, Interior of a pedicle valve, F.4765, holotype.

Fig. 5. *Syringothyris bifida* sp. nov. 5, Interior of brachial valve, F.6040. Note arrangement of muscle scars.

Fig. 6. *Peruvipira* cf. *kuttungensis* sp. nov. Specimen destroyed by fire.



CAMPBELL, Carboniferous fossils

vanian species of North America not only by the differences in shell structure mentioned above, but also by the form of its auricles and the arrangement of its ornament. *L. araneosus* Chronic, from the middle Pennsylvanian of Peru, has a totally different costation. There is no comparison with either *L. nitidus* of the British Westphalian or the *L. newelli* of the American Mississippian.

Genus CYPRICARDINIA Hall 1959

Type species *C. lamellosa* Hall, Devonian, North America.

? *Cypricardinia* sp.

Plate 61, figs. 6, 7

Material. F.4921 and F.4035–8, from the beds below the main *Levipustula* bed, near 019840.

Description. Shell modioloid in shape; umbones about one-fifth of total length from anterior edge; moderately biconvex; hinge-line straight to slightly curved, and somewhat more than half the total shell length; extremities of shell well rounded; very feeble rounded ridge extends from umbo to just dorsal of the postero-ventral margin; very faint concavity on central part of some valves; height/length ratio in largest specimens about two-thirds; umbones strongly inrolled; ornament of rather weak flattened growth laminae, subregularly spaced at about eight per cm. measured from postero-ventral extremity along ridge toward umbo; laminae scarcely perceptible near umbo; discontinuous radial lirae on posterior two-thirds of shell; hinge-plate narrow and slightly thickened; posterior ligament groove long and shallow; right valve with deep socket flanked on either side by a single sharp tooth, just in front of umbo; near posterior extremity of hinge is elongate socket between two lamellar teeth, and a very weak short socket immediately below its posterior extremity; muscle scars and pallial line not known.

Remarks. Only one specimen, F.4921, remains intact, the others having been destroyed or partly destroyed by fire. The remaining specimen is a young right valve, in which the lower posterior socket is almost imperceptible.

The generic assignment is tentative. The type species is from the North American Devonian, and apparently no posterior teeth have been observed in it. Newell (1955) has referred Greenland Permian specimens which have two or three lamellar posterior teeth to *C. ? permica* Licharew, though he points out that Licharew (1931) has concluded that the 'Upper Palaeozoic shells commonly referred to *Cypricardinia*, may differ considerably from the Devonian genotype'.

The specimens herein described differ further from most of the Devonian and Permian species in having much weaker concentric ornament. In this they are like *C. carbonaria* Meek, from the Pottsville formation of Ohio.

Genus SANGUINOLITES M'Coy 1844

Type species *Sanguinolaria? angustata* Phillips, probably from the Viséan of Yorkshire.

Remarks. It is with some doubt that this specimen is referred to *Sanguinolites*, since it is unusual for the anterior muscle scars to be paired in members of that genus. However, Hind (1900, p. 388) records that on *S. plicatus* (Portlock) the deep anterior scar is

'surmounted by an accessory muscle-scar, which is smaller, and lies between it and the umbo'.

? *Sanguinolites* sp.

Plate 61, fig. 8

Material. F.4546 Booral Formation, below the main *Levipustula* bed, near 019840.

Description. Shell approximately equivalve; pre- to post-umbonal length ratio 2/9; height/length ratio 2/5, and height/thickness between 5/6 and 1; hinge-line long and straight and, judging from the growth-lines, is about one-half the total shell length; anterior umbonal slope slightly concave; anterior extremity abruptly rounded; posterior umbonal slope long, straight, sharp, and equal to four-fifths of the posterior length of the shell; posterior outline gently convex and oblique between the hinge and the postero-ventral margin, where it is sharply deflected to the ventral edge; moderately angular keel separates off a flattened posterior face on which are two very weak ridges; lower ridge, the stronger of the two, reaches to within 1 cm. of the umbo, and the almost imperceptible upper one is confined to the posterior third of the face; central part of each valve slightly depressed, making the ventral edge gently concave; lunule small; escutcheon elongate and deep; hinge edentulous.

Ventral anterior adductor scar irregularly angular in shape, deeply impressed, and placed up against the antero-dorsal margin; small flange at its posterior edge; dorsal anterior scar three times as long as high, deeply impressed, and only one-third the area of its neighbour from which it is separated by only 0.5 mm.; posterior adductor scar very slightly impressed, sub-rhombic in outline, and situated with its mid-ventral point on the keel about 7 mm. from the postero-ventral tip of the shell.

Remarks. In shape this specimen is near to *Pleurophorus tropidophorus* (Meek) from the Pottsville Formation of Ohio. Demanet (1943) has figured a form which he refers to *Sanguinolites tropidophorus* (Meek) from the Wn3a of Belgium. Morningstar (1922) considers the species to be a true *Pleurophorus* though she makes mention of neither the dentition nor internal structure. Shimer and Shrock (1944) also leave it in the same genus. Demanet offers no reason for his generic assignment and does not comment on the dentition or the interior. Hence it is not possible to make definite comparisons.

Genus POSIDONIA Bronn 1828

Type species *P. becheri* Bronn, Lower Carboniferous, Germany.

Posidonia sp.

Material. F.4039, from the beds below the main *Levipustula* bed near 019840.

Description. Shell large, c. 50 mm. long and c. 40 mm. along hinge; valves moderately convex; umbones c. 10 mm. behind anterior extremity, of moderate height, and not incurved; angle between hinge-line and line joining umbo to postero-lateral extremity, c. 60°; posterior auricle large and separated from body of valve by gradual change in slope; anterior auricle moderately large, with a concave dorsal edge, and formed of thickened shell material; four to five major concentric folds in shell per cm. on umbonal portions; several weaker folds between major ones; ligament area of left valve markedly

triangular, planar, and ornamented only with growth-lines; hinge edentulous; shell substance thin.

Remarks. The umbo of this specimen is situated slightly farther toward the anterior than the limit set for *Posidonia* by Ramsbottom (1959). However, it is not as far forward as that of most species of *Caneyella*, and in the absence of any sign of radial ornament I have left the specimen in *Posidonia*.

Class GASTROPODA

Superfamily PLEUROTOMARIACEA Swainson 1940

Genus PERUVISPIRA Chronic 1953

Type species *P. delicata* Chronic, lower Permian, Peru.

Remarks. The relationships of this genus have been discussed by Dickins (1961).

Peruvispira kuttungensis sp. nov.

Plate 56, figs. 10-17

Holotype. F.4935; paratypes F.4935A and F.4937 from the Booral Formation near 018859.

Description. Shell much larger than type species, specimens up to 20 mm. high being quite common; turbinate in form, with seven or eight whorls at adult stage; upper whorl surface flat to slightly convex at all stages, and lower surface strongly convex; relatively large peripheral selenizone slightly concave and bounded top and bottom by sharp prominent carinae; occasional specimens with a very low ridge below the lower carina; sutures not deeply impressed, and situated a short distance below selenizone of preceding whorl at all growth stages, distance increasing with each successive whorl; adults definitely anomphalous, though false umbilicus sometimes present; specimens with only five whorls developed also without an umbilicus; nucleus not clearly observed, but probably rather flat; upper whorl surface ornamented with sharply accentuated growth lamellae, moderately convex toward the mouth over most of their course, but deflected sharply adapically just above the selenizone; immediately beneath selenizone lamellae comparable in size with those above, but rapidly become less pronounced and more crowded toward shell base; lamellae either swing forward for a very short distance just under selenizone, and then turn down vertically, or run down almost vertically from the start, finally being deflected backwards in a strongly arched fashion to the axis; selenizone crossed by numerous much finer, but nevertheless quite prominent, sharp crescentic lunulae, numbering five to nine per mm. on the later whorls, but locally crowded together and numbering twelve or thirteen per mm.; form of slit unknown; columellar lip thickened and reflected on itself; no parietal inductura; outer lip plain; pleural angle averages 55°.

Number of lamellae per mm. on middle of upper face

<i>Specimen</i>	<i>Final whorl</i>	<i>Second last</i>	<i>Third last</i>	<i>Fourth last</i>
1	3 to 4	3 to 4	5 to 6	6
2	..	4	5	..
3	..	3	4	6

Remarks. The present species has been placed in this genus with some confidence, even though it is much larger than the type species, the form of the slit has not been observed, the pleural angle is larger, and the ornament coarser.

Occasional specimens found in the fine-grained rocks of the formation are one whorl larger in size, and have much finer, less pronounced lamellae, there being about six per mm. on the last whorl. This is possibly a specific difference, but since the available material is very badly preserved no new species is erected.

Peruvispira cf. kuttungensis Campbell

Material. F.4984, and several other specimens since destroyed by fire, from the Isaacs Formation near 987823.

Remarks. These specimens have a range of variation comparable to that of the types, but they are too poorly preserved for accurate identification.

Localities and repositories. All grid references to localities in the text are to the Dungog One Mile to the Inch Military Map. All specimen numbers refer to the University of New England Collections unless otherwise stated.

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THE ANCHORAGE OF ARTICULATE BRACHIOPODS ON SOFT SUBSTRATA

by M. J. S. RUDWICK

FOSSIL articulate brachiopods are often abundant in rocks that appear to have accumulated as soft sediments. In some species there is evidence (e.g. a diminutive or plugged foramen) that the pedicle atrophied during ontogeny and that the adult shells were free-living. But in many other species a large foramen is found in all sizes of shell, and it is evident that the pedicle was functional throughout life; yet there may be no evidence of any firm material—except other shells—to which the pedicle could have been attached. Elliott (1956) has commented on the ease with which brachiopod shells can be transported after death, without damage, even by gentle currents. It is therefore possible that in some cases these fossil occurrences may be the result of shells having drifted, e.g. from a rocky environment near a shoreline into an offshore area in which soft sediment was accumulating. But it is also possible that such brachiopods may have lived on the soft sediment in which their shells are now preserved. Most articulate brachiopods living at the present day seem to require some hard and firm substratum (e.g. rock or shell) for attachment. But exceptions to this rule show that it is possible for the pedicle to obtain satisfactory anchorage in soft materials; and this type of attachment may have been much more common in the past. (The ability of inarticulates (e.g. *Lingula*) to anchor in soft substrata is well known; but their pedicles are not homologous to those of articulates, and differ completely in their structure.) Some records of the attachment of articulates to soft materials are given below.

The abyssal brachiopod *Chlidonophora cluni* Blochmann was dredged from *Globigerina* ooze, and was found to have an exceptionally long pedicle, dividing distally into fine rootlets attached to *Globigerina* shells. Blochmann (1906) inferred from this that the shell had been rooted in the soft ooze by this unusual pedicle. The pedicle of *Terebratulina* also shows a tendency to split distally into short rootlets (Ekman 1896), which may be attached to small shell-fragments in a fine shell gravel.

Gray (1872) noted that in *Kraussina rubra* (Pallas) from South Africa the pedicle is usually attached to the stem of a large alga or to an ascidian. A similar habit has been observed occasionally in other species. Attachment to algae was noted by Forbes in *Megathiris*, and by Jeffreys in *Terebratulina* (see Gray 1872). I have found specimens of *Terebratella* (*Waltonia*) *inconspicua* (Sowerby) attached to ascidians on rocky shores in New Zealand, and Ekman (1896) noted the same habit in *Terebratulina*. In an assemblage of *Terebratella* (*Magasella*) *sanguinea* (Leach), dredged from a muddy bottom at about 54 fathoms (100 m.) off Oamaru in New Zealand, all the shells were attached by their pedicles to the tangled 'horny' tubes of the chaetopterid worm *Phyllochaetopterus socialis* Claparède. Neither algae nor ascidians nor 'horny' worm-tubes would be

fossilized under normal circumstances. Therefore all these occurrences, if they were fossilized, would yield no trace of the substratum used for anchorage.

These examples suggest that the pedicles of many fossil brachiopods may have been able likewise to anchor the shells either (*a*) into bottoms composed of soft unconsolidated sediment, or (*b*) on to organic materials that would normally escape fossilization. Therefore it may not be necessary to invoke drifting as an explanation of the occurrence of pediculate fossil brachiopods in rocks that accumulated as soft sediments. Such brachiopods may often be undrifted life-assemblages, fossilized in the environment in which the living population existed.

The fact that living brachiopods can be attached to organic materials may also help to explain the 'nests' of fossil brachiopods so common in certain rocks (e.g. Hallam 1955, 1960). It is possible that each 'nest' may represent a colony of brachiopods that was attached to a small patch of organic material, e.g. to the stem of a single large alga. The shells as fossilized might represent either (*a*) an assemblage of shells which fell off the supporting material into the sediment after death, and gradually accumulated there; or (*b*) a living population suddenly annihilated by the collapse of the supporting material into the sediment. In this connexion it is noteworthy that in the Red Crag brachiopods have been found in similar clusters, in each of which the original material of attachment—a large stone—is still preserved in position (Bell 1872, pp. 191–2).

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SHELL DEVELOPMENT IN *SPIRIFER TRIGONALIS* FROM THE CARBONIFEROUS OF SCOTLAND

by GRACE M. DUNLOP

ABSTRACT. The neotype of *Spirifer trigonalis* (Martin) is described and a group of spiriferids from the Carboniferous Limestone Series of Lanarkshire, displaying wide variation in external form, is assigned to this species.

The microstructure and distribution of lamellar, fibrous, and inner columnar layers is described. Extracellular secretion of the columnar layer is postulated. Interlayering of fibrous and columnar layers is attributed to pauses in growth, accompanied by retraction of the mantle and a consequent change in distribution of the layers. The distribution and development of internal plates is described. Teeth, dental flanges, delthyrial plate, dental sockets, crura, and cardinal process appear in the neanic shell and continue to grow. The delthyrial plate covers early dental flanges; similarly the cardinal process buries early socket cavities and crural bases. Dental plates appear first in the ephebic shell and contribute to the apical infilling in the adult shell.

SINCE Carpenter (1853, p. 25) described the microstructure of the spiriferid shell and speculated on its mode of origin growth studies have been few, and microstructure has been generally neglected in all but the punctate genera. Only Miloradovitch (1937) recognized the value of shell structure in reconstructing the general pattern of shell development. The detailed study of the shell in one species, *Spirifer trigonalis* (Martin), has shown that in the microstructure there is much evidence of the ontogeny of the shell and some suggestion of its mode of origin.

As no description of the species has been given since the validation (International Commission 1956) of the name *trigonalis* a systematic description follows.

SYSTEMATIC DESCRIPTION

Family SPIRIFERIDAE King 1846, p. 28

Subfamily SPIRIFERINAE Schuchert 1913, p. 410

Genus SPIRIFER Sowerby 1816, p. 125, pl. 270

Type species *Spirifer striatus* (Martin)

Remarks. The internal characters of the genus are unknown, not being shown in the neotype (International Commission 1956, p. 89). The name *Spirifer* is retained here to signify a costate spire-bearer with transverse form, though *S. trigonalis* differs from *S. striatus* in the details of shell profile, rib and furrow shape, and microsculpture.

Spirifer trigonalis (Martin)

Neotype—Plate 64, 1–3

The trivial name *trigonalis* was proposed by Martin (1809, pl. 36) in the combination *Conchyliolithus Anonites trigonalis*. Sowerby (1818–21, p. 117, pl. 275) assigned the species to his genus *Spirifer*. Sowerby's interpretation of the species, however, differed from Martin's original description. When, by the ruling of the International Commission on Zoological Nomenclature (1950), *trigonalis* was invalidated, Muir-Wood (1951)

considered it undesirable to refer *trigonalis* to Sowerby and permission was sought and obtained from the International Commission (1956) to validate *trigonalis* Martin 1809.

Neotype. Since the type specimen illustrated by Martin (1809, pl. 36) is lost a neotype was selected (International Commission 1956, pp. 112–13). It is a specimen in the British Museum (Natural History) BB 7340 (plate 64, 1–3) which was figured by Davidson (1858, pl. 5, fig. 33 and 1863, pl. 50, fig. 4).

Occurrence. The neotype is from the North Greens Limestone of the Lower Limestone Group, Carboniferous Limestone Series, at Cousland, Dalkeith, Midlothian. The species is thus no longer based on material from Derbyshire.

Diagnosis. Martin's (1809) original diagnosis deals with the general trigonal shape of the shell and the costation of sulcus and flanks. An examination of the neotype and of topotype material in the collections of the Geological Survey, Scottish Office (B 1735d, B 1787d, T 3277F), reveals the following additional characters: the ribs are rounded; very fine longitudinal striations produce a twilling of the growth-lines. Dental plates short, dental flanges present, ventral septum low, convex delthyrial plate in apex of delthyrium (Pl. 65, fig. 7).

Description of neotype

Length	19.8 mm.
Maximum width	23.8 mm.
Hinge width	21.35 mm.
Thickness	12.8 mm.

Shell subtriangular, biconvex, moderately inflated. Width/length ratio 1.2; maximum width anterior to hinge-line, greatest thickness near mid-length. Cardinal angle obtuse. Ventral umbo pointed, overhangs interarea; dorsal umbo low, rounded. Ventral interarea delimited by beak ridges; delthyrium edged by dental ridges, delthyrial plate at apex. Denticle tracks, about twenty-four, underlying lamellar layer. Dorsal interarea low and notothyrium obscured by detritus.

Ventral sulcus wide and shallow, with gently sloping sides and labial extension. Dorsal fold rises sharply from the flanks. Fold and sulcus originate at about 1 mm. from umbo. Anterior commissure uniplicate.

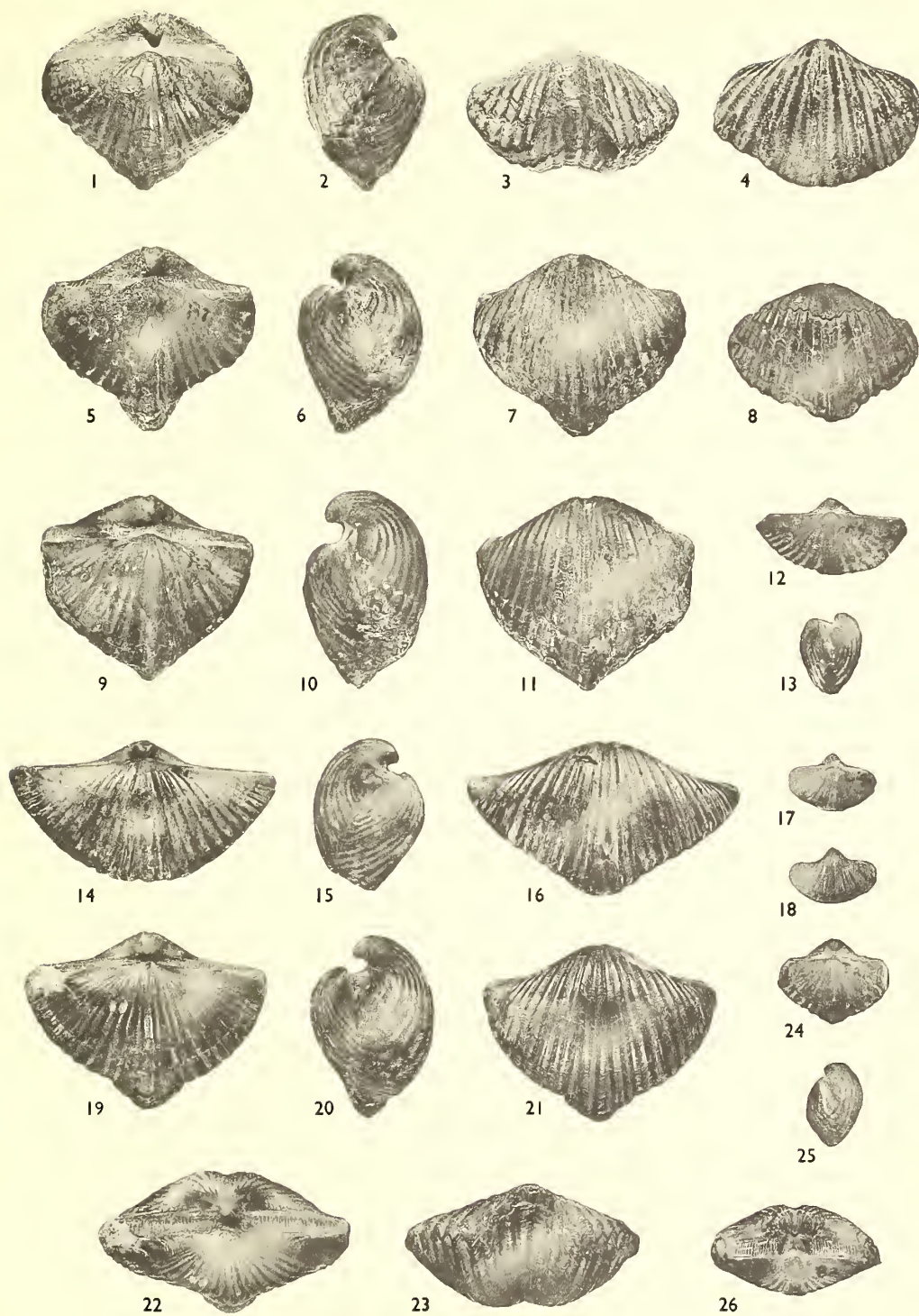
Ribs on flanks, from seven to nine in number, strong, broad and rounded, separated by rounded furrows. Weakly developed incipient ribs at cardinal extremities. The ribs immediately adjacent to both fold and sulcus show dichotomy. Also, the third rib to the right of the dorsal fold, and the corresponding rib in the pedicle valve, divide near the anterior margin.

EXPLANATION OF PLATE 64

Spirifer trigonalis (Martin). All figures natural size, except 4.

Figs. 1–3. Neotype (British Museum BB 7340); North Greens Limestone of Lower Limestone Group; Cousland, Dalkeith, Midlothian. 1, Dorsal view; 2, Lateral view; 3, Anterior view.

Figs. 4–26. *Spirifer trigonalis* (Martin); Douglas Main Limestone of Lower Limestone Group; Brockley, Lanarkshire. All specimens in Hunterian Museum, Glasgow. 4, Ventral view showing many growth-lines. L 3636. 5–7, Dorsal, lateral, and ventral views. L 3633. 8, Ventral view showing four prominent growth-lines. L 3640. 9–11, Dorsal, lateral, and ventral views. L 3632. 12, 13, Dorsal and lateral views. L 3637. 14–16, Dorsal, lateral, and ventral views. L 3635. 17, 18, Dorsal and ventral views. L 3638. 19–23, Dorsal, lateral, ventral, posterior, and anterior views. L 3641. 24, 25, Dorsal and lateral views. L 3639. 26, Posterior view showing denticle tracks on interarea. L 3634.



In ventral sulcus, two lateral ribs split off from each of the two bounding ribs. A median rib becomes very prominent anteriorly. The ribs on the fold correspond in pattern, with two lateral ribs on each side and a broad central rib with a median furrow.

Many growth-lines visible, two notably prominent and several well marked near anterior margin. Growth-lines also visible on ventral inter-area. No microsculpture is present due probably to the state of preservation of the specimen.

Internal characters are unknown.

Comparison with other species. The field of *Spirifer trigonalis* became widely comprehensive during the nineteenth century with the result that many of the specimens assigned to the species by Davidson (1858–63, pl. 5, fig. 28; pl. 50, figs. 5–8) and de Koninck (1887, pl. 26, figs. 5–8; pl. 28, figs. 7, 27, 31) are quite unlike the neotype both in shape of shell and shape and number of ribs. The specimens recognized as *S. trigonalis* var. *lata* by Schellwien (1892, p. 46, pl. 5, figs. 10–12), Scupin (1900, pl. 9, fig. 7), and Rakusz (1932, p. 72, pl. 2, fig. 34) are probably outside the range of variation of the species.

The Russian specimens described by Trautschold (1876, p. 351, pl. 8, fig. 3), Lebedew (1929, p. 256, pl. 10, fig. 5), and Rotai (1931, pp. 77 and 123, pl. 10, fig. 4) seem to be more closely allied. Schwezow (1925, pp. 156 and 178, pl. 4, fig. 2) recognizes *S. trigonalis* var. *typica* from the Moscow basin which is close to the neotype.

Semichatova (1941, p. 156 in translation) erected the species *S. pseudotrigonalis* for forms which 'could be probably regarded as a local variety of *Spirifer trigonalis*' (p. 157). She shows that there are some small differences in external shape between her specimens and Martin's holotype. Now that the internal characters of the pedicle valve in the topotype material of *S. trigonalis* are known (Plate 65, fig. 7), and it is found that they closely resemble those of *S. pseudotrigonalis* (Semichatova 1941, pl. 8, figs. 1a, b, 2, 3a, 4; pl. 9, figs. 1, 2) in the details of the dental plates, dental flanges, septum and delthyrial plate, the similarity of the two species is more striking and the question of their synonymy arises. *S. pseudotrigonalis*, by original diagnosis (Semichatova 1941, p. 156), has non-dichotomous ribs, whereas the neotype of *S. trigonalis* shows dichotomy; but *S. pseudotrigonalis* var. *furcata* Semichatova (1941, p. 157) is distinguished by 'the bifurcation of plications taking place both in the sinus and on the lateral portions of the shell', and it seems probable that in this wider sense *S. pseudotrigonalis* is a synonym of *S. trigonalis*. In external form *S. pseudotrigonalis* is no less like *S. trigonalis* than are some of the variants of *S. trigonalis* now demonstrated. Indeed several of the other species distinguished by Semichatova (1941), in the *S. pseudotrigonalis* group, on the basis of size, shape, shape of fold and sulcus, and details of rib patterns present a range of variation in external form similar to that now shown in *S. trigonalis* and their validity is therefore doubtful: they may be no more than named variants of *S. trigonalis*.

SPECIMENS FROM BROCKLEY

The specimens used in the study of the development of the shell (Plate 64, figs. 4–26) are from the Douglas Main Limestone of the Lower Limestone Group, in the Poncil Water, at Brockley, 1½ miles south of Coalburn, Lanarkshire. One hundred and seventeen specimens were collected and are now in the Hunterian Museum, Glasgow (figured specimens nos. L 3632–L 3641).

Ninety-six of the specimens are sufficiently well preserved to be studied biometrically. They were all collected from one exposure but they were distributed through about 20 feet of limestone so they cannot be regarded as strictly contemporaneous members of a single population. Also, the presence of separate valves shows that the specimens were probably transported before burial and do not represent successive populations. The specimens show wide variation in shell shape, the variation being continuous (text-fig. 1*b-e*). The statistical measures of the sample are given in Table 1; the high coefficients

TABLE 1. *Statistical measures of the specimens of Spirifer trigonalis (Martin) in the collection from Brockley, Lanarkshire*

Character	Number of specimens	Range	Mean	Standard deviation
Hinge width (mm.)	72	9.5-39.3	20.4	7.46
Maximum width (mm.)	53	11.0-39.3	21.3	6.98
Length (mm.)	72	7.2-28.1	15.6	5.79
Thickness (mm.)	87	5.2-18.2	10.8	3.59
Maximum width	51	1.11-1.98	1.46	0.179
Length				
Thickness				
Length	87	0.59-0.82	0.69	0.0477
Number of ribs				
Length (mm.)	71	0.64-1.89	1.11	0.232

$$\text{Coefficient of correlation } \frac{\text{hinge-width}}{\text{length}} = 0.77$$

$$\text{Coefficient of correlation } \frac{\text{thickness}}{\text{length}} = 0.90$$

of correlation showing that it is probable that a single species is represented. The scatter diagram and the unimodal histograms (text-fig. 1) present the same evidence.

EXPLANATION OF PLATE 65

Microstructure of shell in *Spirifer trigonalis* (Martin).

Figs. 1-3 and 5-7 are thin sections photographed under crossed nicols. Figs. 1-6: specimens from Douglas Main Limestone, Brockley, Lanarkshire.

Fig. 1. Transverse section showing growth-line in columnar layer, $\times 30$.

Fig. 2. Oblique transverse section showing dental flanges and enveloping dental plates, $\times 36$.

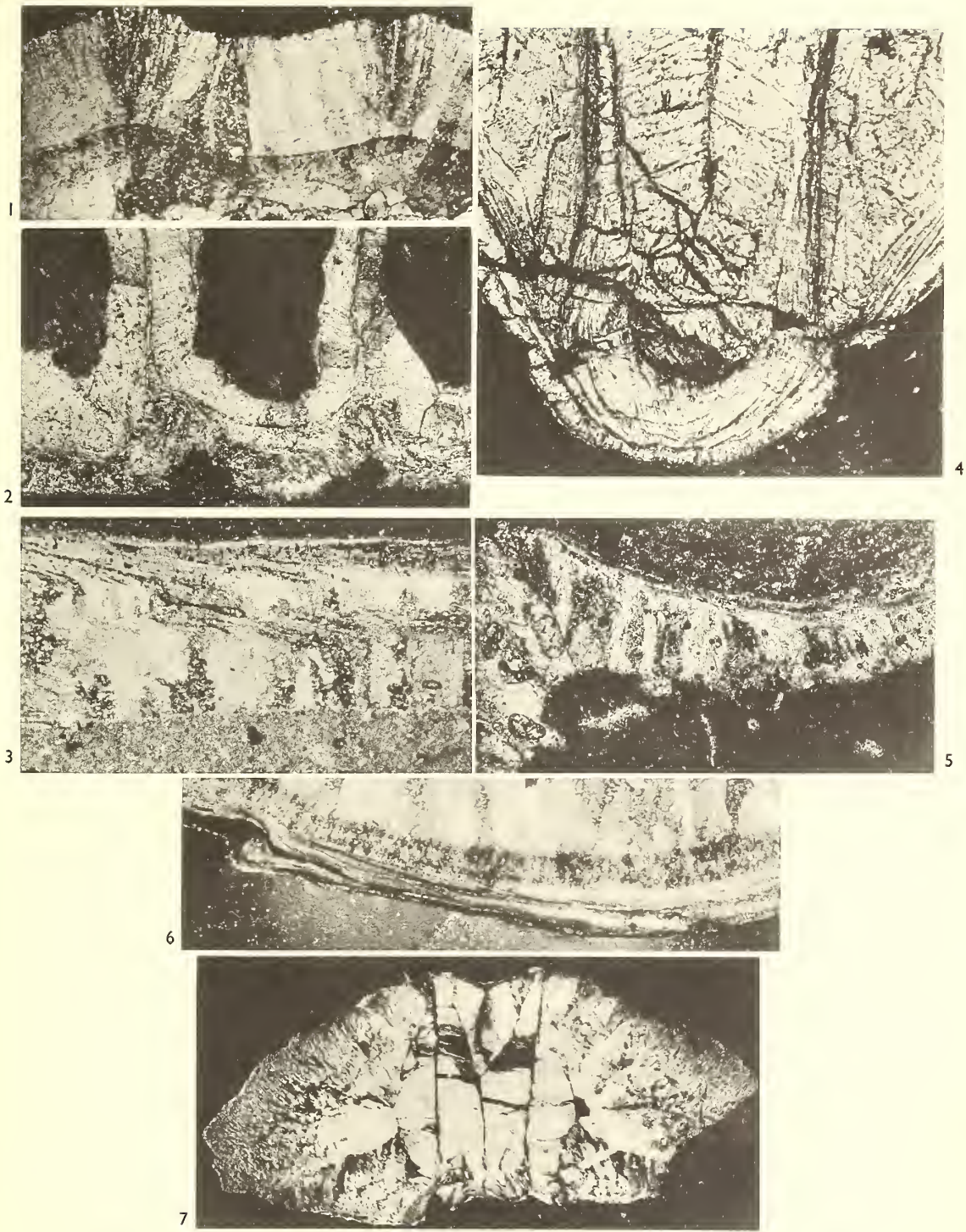
Fig. 3. Longitudinal section showing external lamellar layer and interlayering of fibrous and columnar layers, $\times 50$.

Fig. 4. Cellulose peel of oblique transverse section in apex of pedicle valve showing dental plates and apical infilling, $\times 40$.

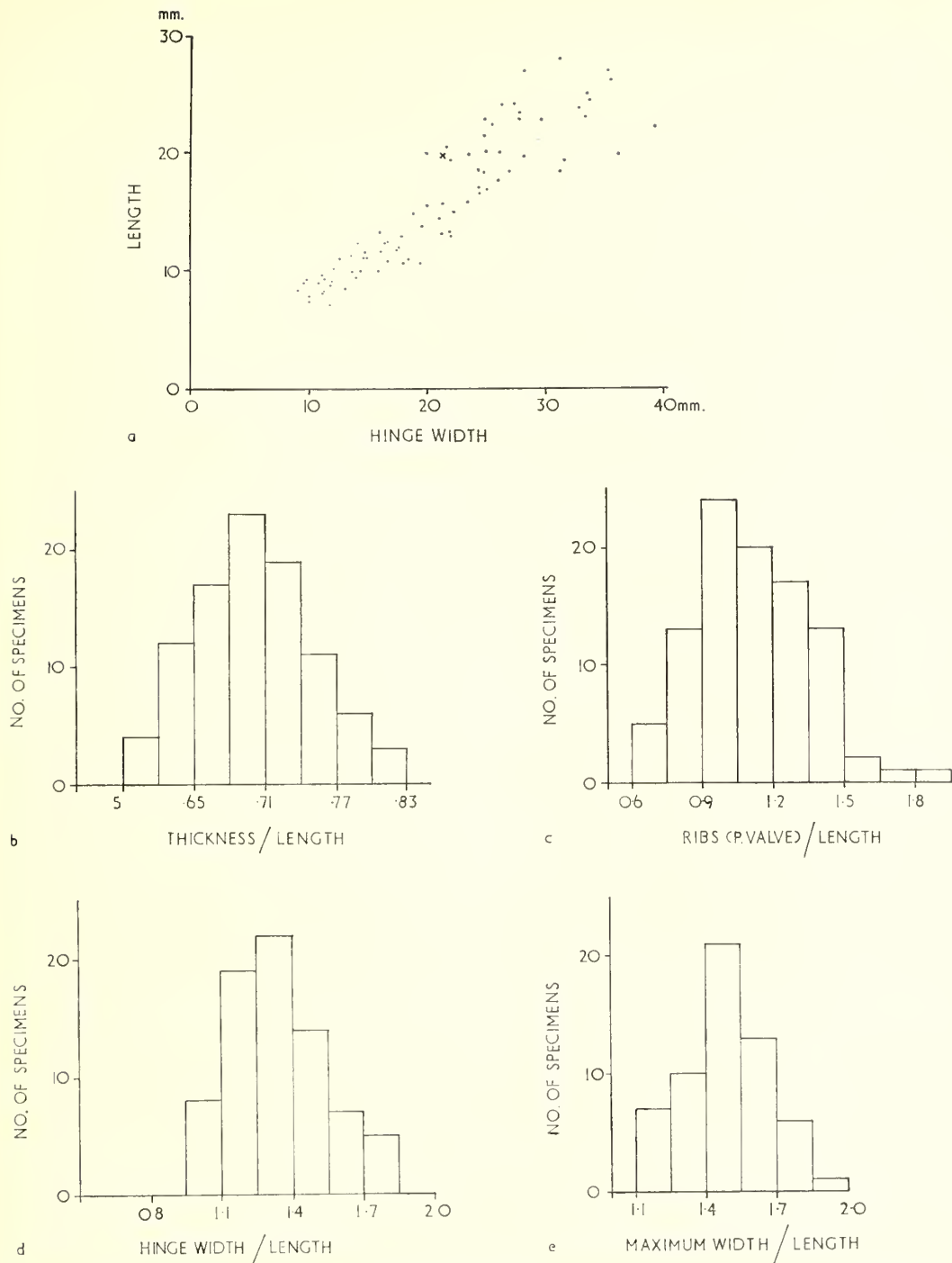
Fig. 5. Longitudinal section of ventral interarea showing fibrous and columnar layers and a remnant of lamellar layer, $\times 25$.

Fig. 6. Longitudinal section showing external growth-line and corresponding internal growth-line in fibrous layer, $\times 17$.

Fig. 7. Specimen from North Greens Limestone, Cousland, Dalkeith, Midlothian. T3277F Geological Survey Collections, Edinburgh. Transverse section of pedicle valve showing dental plates, dental flanges, and a remnant of delthyrial plate, $\times 8$.



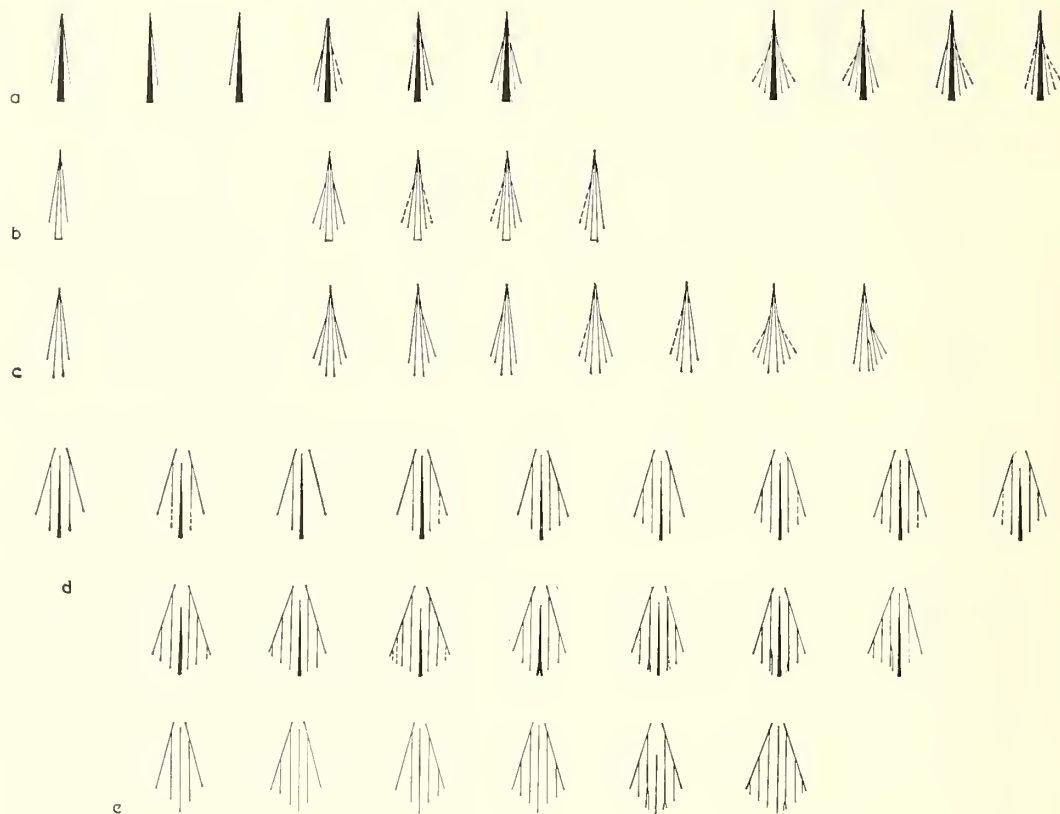
DUNLOP, *Spirifer trigonalis* (Martin)



TEXT-FIG. 1. *Spirifer trigonalis* (Martin) from Brockley, Lanarkshire. *a*, Scatter diagram, x=neotype of species. *b-e*, Histograms showing frequency distribution of various shell ratios; *b*, 95 specimens; *c*, 96 specimens; *d*, 75 specimens; *e*, 58 specimens.

Variation in such characters as the number of ribs on fold and sulcus (text-fig. 2), the height and width of fold and sulcus, and the shape of cardinal angles are considered to be intraspecific.

Comparison of neotype with Brockley specimens. When plotted on the same diagram the



TEXT-FIG. 2. Variation in the ribs of fold and sulcus in *Spirifer trigonalis* (Martin). *a-c*, Ribs on fold; *a*, median rib undivided; *b*, median rib with longitudinal furrow; *c*, median rib divided. *d-e*, Ribs in sulcus; *d*, median rib prominent; *e*, median rib not prominent. Broken lines indicate faint ribs, and heavy lines indicate prominent median ribs.

neotype of *Spirifer trigonalis* lies on the fringe of the scatter diagram of the Brockley specimens (text-fig. 1*a*), though it falls within the range of variation of the Brockley specimens as shown by the histograms.

Table 2 shows a comparison of the neotype with the Brockley sample, in which the neotype is regarded as a sample of size 1, with mean values those of the neotype. Since t , difference between means/standard error of difference of means, does not exceed 1.96, the means do not differ significantly at the 5 per cent. level. The Brockley specimens are thus regarded as belonging to *Spirifer trigonalis*.

TABLE 2. *Comparison of the specimens from Brockley with the neotype of Spirifer trigonalis (Martin)*

Character	Standard error of difference of means	$t = \frac{\text{Difference between means}}{\text{Standard error of difference of means}}$
	$\sigma \sqrt{\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}$	
Maximum width	0.1938	1.34
Length		
Thickness	0.0498	0.8
Length		
Number of ribs	0.2975	1.02
Length		

DEVELOPMENT OF EXTERNAL FORM

The study of external growth-lines reveals changes in shell ratio (hinge width/length) during development. The shell becomes longer relative to its width in the later growth stages (text-fig. 3a). This change in growth ratio is found in both brachial and pedicle valves and in the interareas (text-fig. 3b). There is also some evidence of an opposite change in growth ratio during early growth stages.

There is considerable variation in the size and proportions of the shell of different individuals when the second change in growth ratio occurs; the width varies between 9.8 mm. and 25.2 mm. and the shell index between 1.5 and 2.1. The graph (text-fig. 3c) illustrates the growth of thirty-one specimens. In a few specimens no change occurs and extremely transverse shells are formed (pl. 64, fig. 14). These produce the skewness in the histograms (text-fig. 1c, d).

In contrast to the variable width/length ratio is the constant thickness/length ratio (text-fig. 1b) which is shown by the high coefficient of correlation (Table 1) and indicates an allometric relationship. Similarly, the ratio hinge width/number of ribs is constant both in the individual and in the collection as a whole (text-fig. 3d) except when dichotomy occurs.

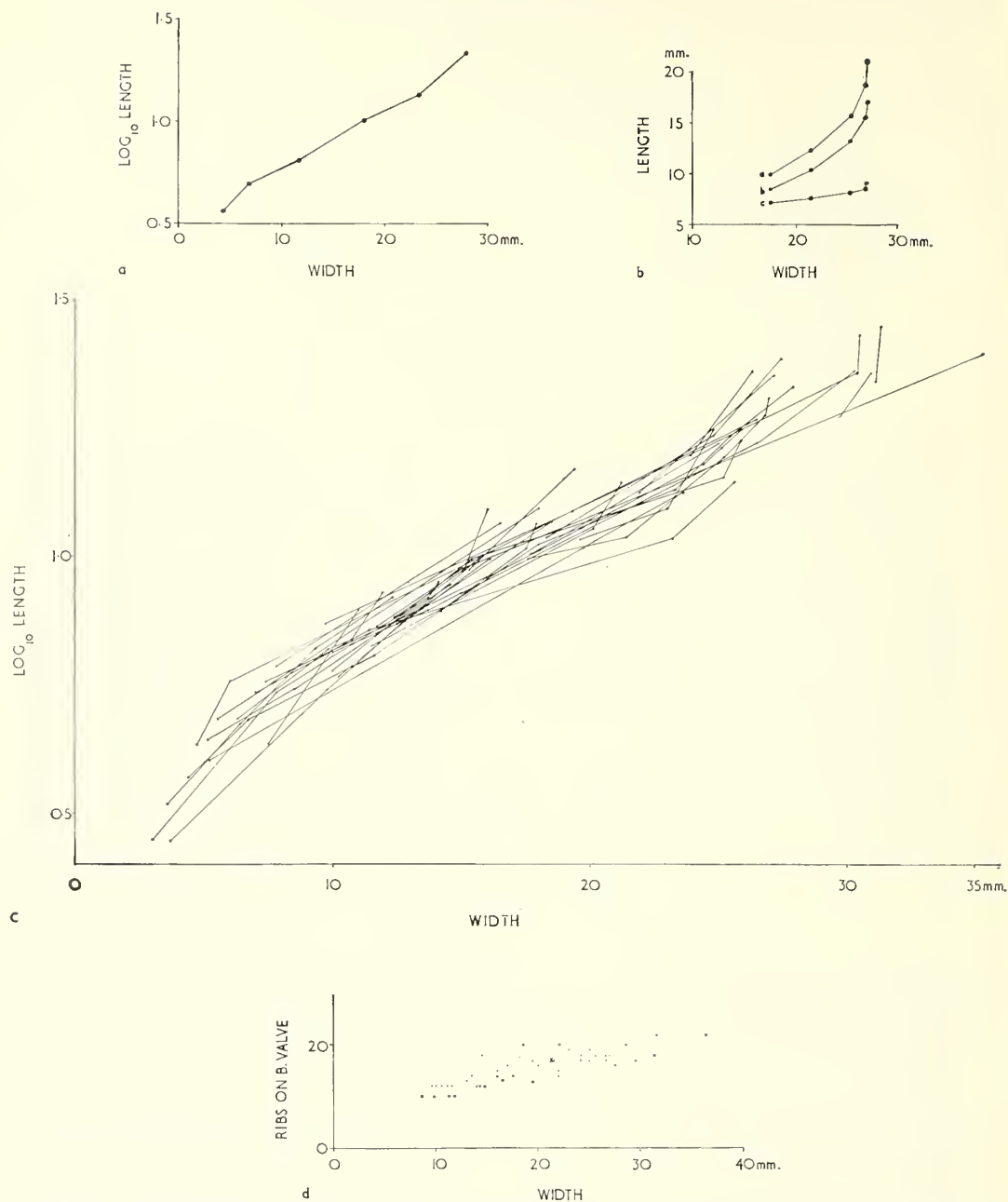
MICROSTRUCTURE OF THE SHELL

Terminology of shell layers. The shell is composed of three layers, all impunctate, the lamellar layer, the fibrous layer, and the columnar layer (text-fig. 4a).

Lamellar layer: this outer, non-fibrous layer, about 0.02 mm. in uniform thickness, extends over the whole surface of the shell.

Fibrous layer: immediately underlying the lamellar layer is the fibrous layer, of variable thickness, composed of long slender fibrous calcite crystals about 0.007 mm. in width. The fibres are perpendicular to the valve margins and are inclined inwards, in an anterior direction, at a low angle.

Some confusion exists about the naming of this shell layer. Thus, Williams (1953, p. 280) refers to the 'fibrous layer' while Cooper (1944, p. 281) uses the term 'prismatic layer' for the same structure. Carpenter (1853, p. 25), who first described this particular microstructure, states that 'the shell is found to consist of flattened prisms' but he does not refer to a 'prismatic layer'. Later, Hall (1867, p. 186) states simply that in *Spirifer*



TEXT-FIG. 3. Growth of the shell in *Spirifer trigonalis* (Martin). *a*, Graph of growth stages in one individual, showing a change in growth ratio at 24 mm. width. *b*, Graphs of growth stages in one individual—*a*, pedicle valve, *b*, brachial valve, *c*, ventral interarea. *c*, Graph of growth of the shell in 31 individuals showing changes in growth ratio during ontogeny. *d*, Scatter plot showing the direct relation between number of ribs and width of hinge in those specimens with no dichotomy of ribs. x=neotype of species.

'the shell substance is fibrous'. The indiscriminate way in which the terms have been used is illustrated in Schuchert's (1913, p. 357) discussion of shell structure. First he mentions a 'thick prismatic layer', then 'fibrous prisms', and finally, referring to the same structure, the 'fibrous layer'. With the description now of another type of prismatic layer in brachiopods, the columnar layer, it is preferable that the term fibrous layer be used for that microstructure in which the slender prisms are arranged at a low angle to the shell surface.

Columnar layer: this term is proposed for an inner prismatic layer which lies over the fibrous layer in some parts of the shell. It is of variable thickness and is composed of short, calcite prisms up to 1 mm. in length and 0.05 to 0.06 mm. in width (text-fig. 4a). The crystals are orientated normal to the shell surface and are elongate in this direction, which is the *c*-axis of the crystal. Their prismatic form is seen in tangential section (text-fig. 4b).

The columnar layer is frequently traversed by lines parallel to the surface of the shell (text-fig. 4c), marked in some cases by inclusions of a fine textured brown substance (pl. 65, fig. 1) and in other cases by cavities in the crystals. These discontinuities are considered to result from pauses in growth; the lines are regarded as growth-lines. They were recorded in Russian spiriferids by Miloradovitsch (1937, p. 526).

Relation of fibrous and columnar layers. The lamellar layer forms a thin film over the entire external surface of the shell and beneath it lies the fibrous layer, very thin at the umbones and increasing in thickness anteriorly. In contrast the columnar layer is confined to the posterior region (text-fig. 5a, b). Internal to the fibrous layer, it is distinctly separate from it, with no gradation between the two (text-fig. 5c). It is concluded that the columnar layer formed later than the fibrous layer, a distinct break occurring between the secretion of the two layers.

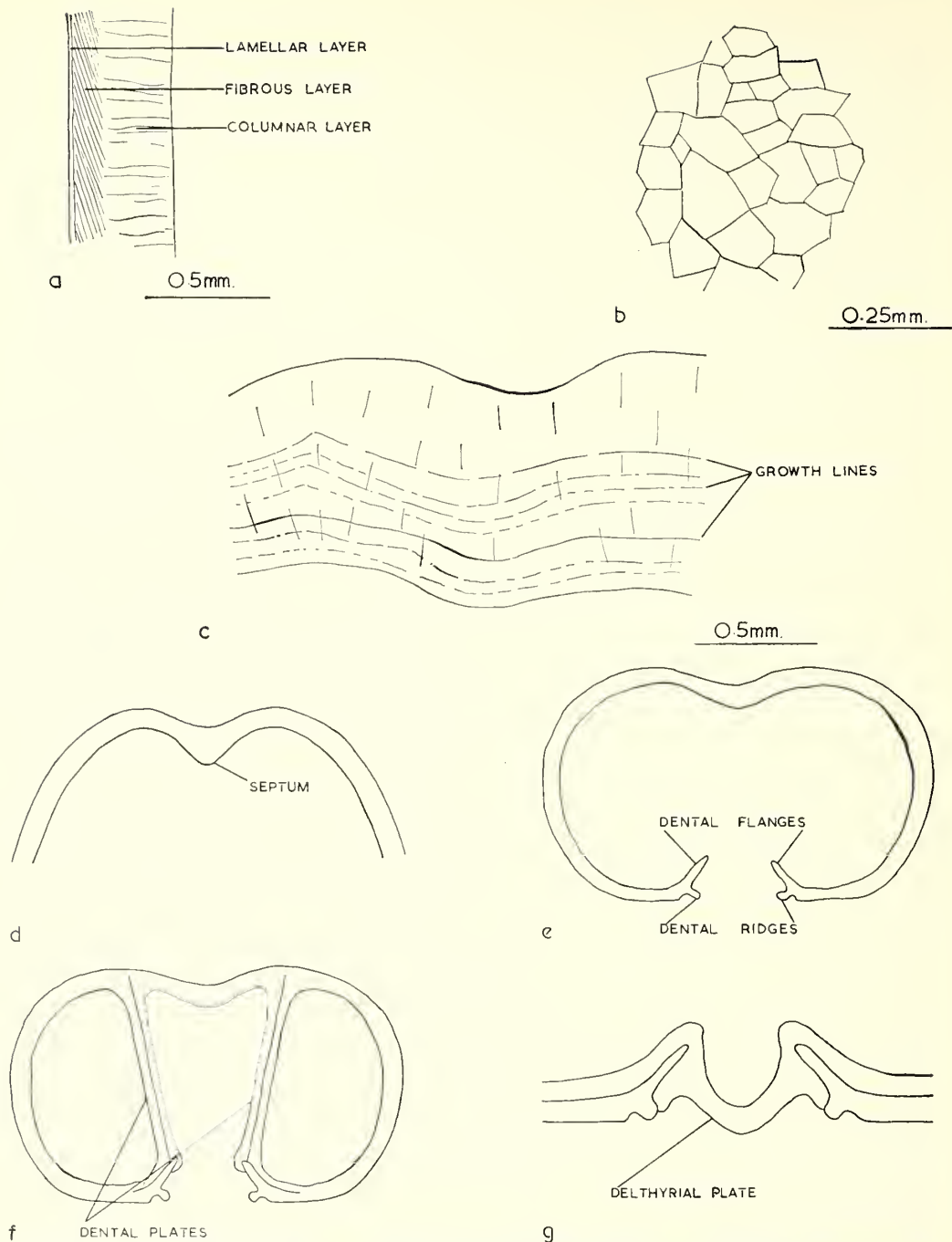
The columnar layer is present in shells not fully grown so its deposition was not merely a gerontic phenomenon. In the neanic shells its distribution is the same as in the adult shell. The deposition of the two types of shell material therefore occurred concurrently in different parts of the shell, the columnar layer gradually spreading anteriorly over the fibrous layer.

The fibrous layer continued to grow in thickness until it was covered by the columnar layer. Its thickest development therefore occurs immediately anterior to the columnar layer (text-fig. 5a). The columnar layer, on the other hand, continued to increase in thickness throughout growth and attains its maximum posteriorly.

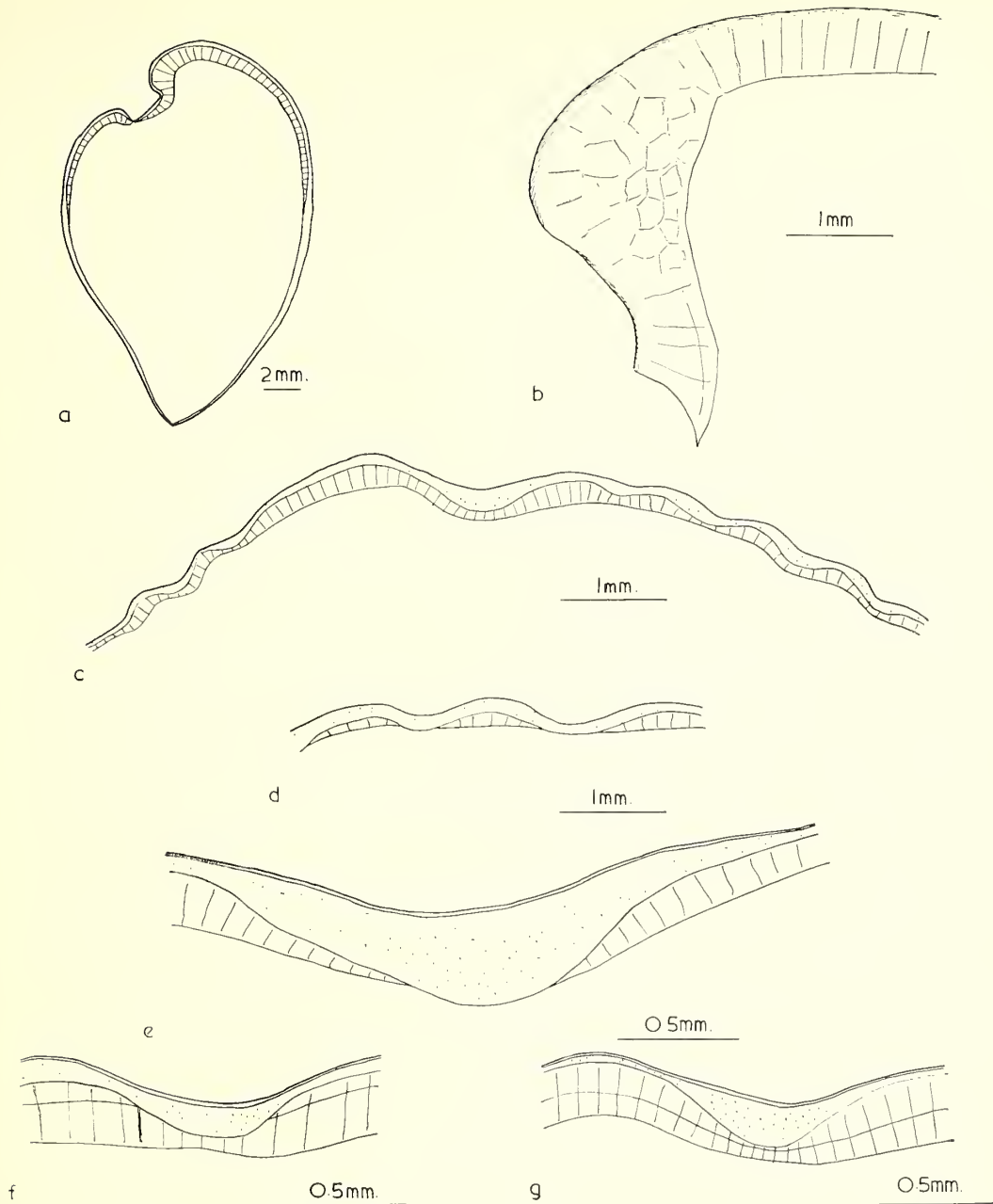
The fibrous layer, growing anteriorly, paralleled the margin of the valve and reflected all the undulations of the surface of the shell. The anterior margin of the columnar layer thus filled in the grooves before extending in an unbroken sheet across the width of the shell. This gradual infilling of the hollows is especially well seen on the flanks of the sulcus where the columnar layer tends to thin out against the fibrous layer before finally overlapping it (text-fig. 5e-g).

The columnar layer thus differs from the fibrous layer in its growth pattern.

In some cases the inner shell layers alternate with each other, fibrous layer occurring internal to columnar layer and columnar layer internal to that again (Pl. 65, fig. 4, text-fig. 6a). Rarely several alternations occur (text-fig. 6d). Such interlayering may occur in any part of the shell where columnar layer normally occurs, and while it is limited in



TEXT-FIG. 4. Microstructure of the shell and the internal plates of the pedicle valve of *Spirifer trigonalis* (Martin). *a*, Lamellar, fibrous, and columnar layers in longitudinal section. *b*, Columnar layer in tangential section. *c*, Columnar layer in transverse section, showing growth-lines. *d-g*, Internal plates of pedicle valves in transverse section; *d*, ventral septum; *e*, dental flanges and dental ridges; *f*, dental plates, dental flanges, and dental ridges; *g*, delthyrial plate, dental flanges, and dental ridges.



TEXT-FIG. 5. Distribution of shell layers in *Spirifer trigonalis* (Martin). *a*, Longitudinal section showing general distribution of fibrous and columnar layers. *b*, Longitudinal section of apex of pedicle valve showing columnar layer of umbonal infilling. *c*, Transverse section of young individual showing columnar layer in posterior part of shell. *d*, Transverse section showing anterior prolongations of columnar layer in the grooves on the inner surface of the shell beneath the ribs. *e*, Transverse section showing columnar layer flanking the fibrous layer of the sulcus. *f*, Transverse section showing columnar layer overlapping the fibrous layer of the sulcus. *g*, Transverse section showing columnar layer thinning against and overlapping the fibrous layer of the sulcus.

longitudinal extent to some 5 mm. it stretches right across the valve. It is clear that in certain circumstances fibrous layer may have been secreted over columnar layer.

The columnar layer may occur only as lenticles in the fibrous layer (text-fig. 6b). In this case the renewed secretion of fibrous layer had occurred in an area where the columnar layer only occupied the hollows of the ribs.

The particular conditions governing the development of interlayering are discovered when the repeated layers are traced anteriorly and posteriorly (text-fig. 7c, d). Anteriorly the outer columnar layer dies out and two sheets of fibrous layer come together separated by a plane of discontinuity in the fibres. When this plane is traced to the surface (Pl. 65, fig. 6, text-fig. 7d) it is found to correspond with an external growth-line. Similarly, when the inner fibrous layer is traced posteriorly from the zone of interlayering it dies out and is replaced by an internal growth-line in the normal layer. Interlayering is therefore consequent on a pause in the growth of the shell.

A growth halt which produced a prominent external growth-line also affected the internal secretion of the shell material. A discontinuity of structure can be traced from the external growth-line posteriorly to the umbo (text-fig. 7b); anteriorly the break occurs within the fibrous layer, posteriorly the break is in the columnar layer and between the two is the zone of interlayering. The interareas also display a narrow zone of interlayering (text-fig. 7e). The growth halt is thus recorded in various ways in all parts of the shell.

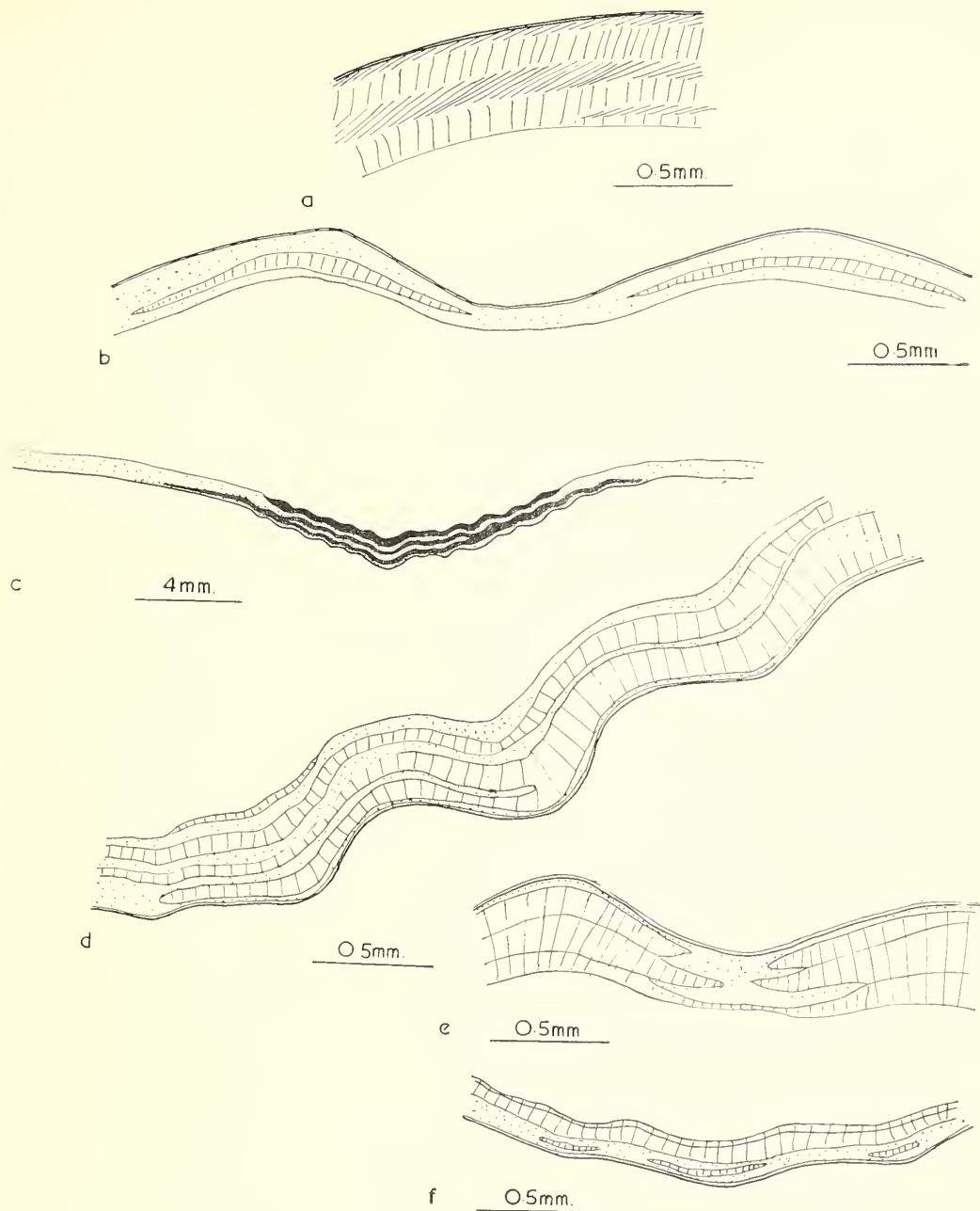
Growth pauses may occur at any stage in the development of the shell, the early ones being recorded only in the posterior parts of the shell. In transverse sections, therefore, the older median part may record more pauses than the younger lateral parts (text-fig. 6c, d).

Late-stage intermittent growth, often found in larger specimens, did not cause any considerable interlayering, though duplication of the fibrous layer anteriorly, and growth-lines in the columnar layer posteriorly, are observed.

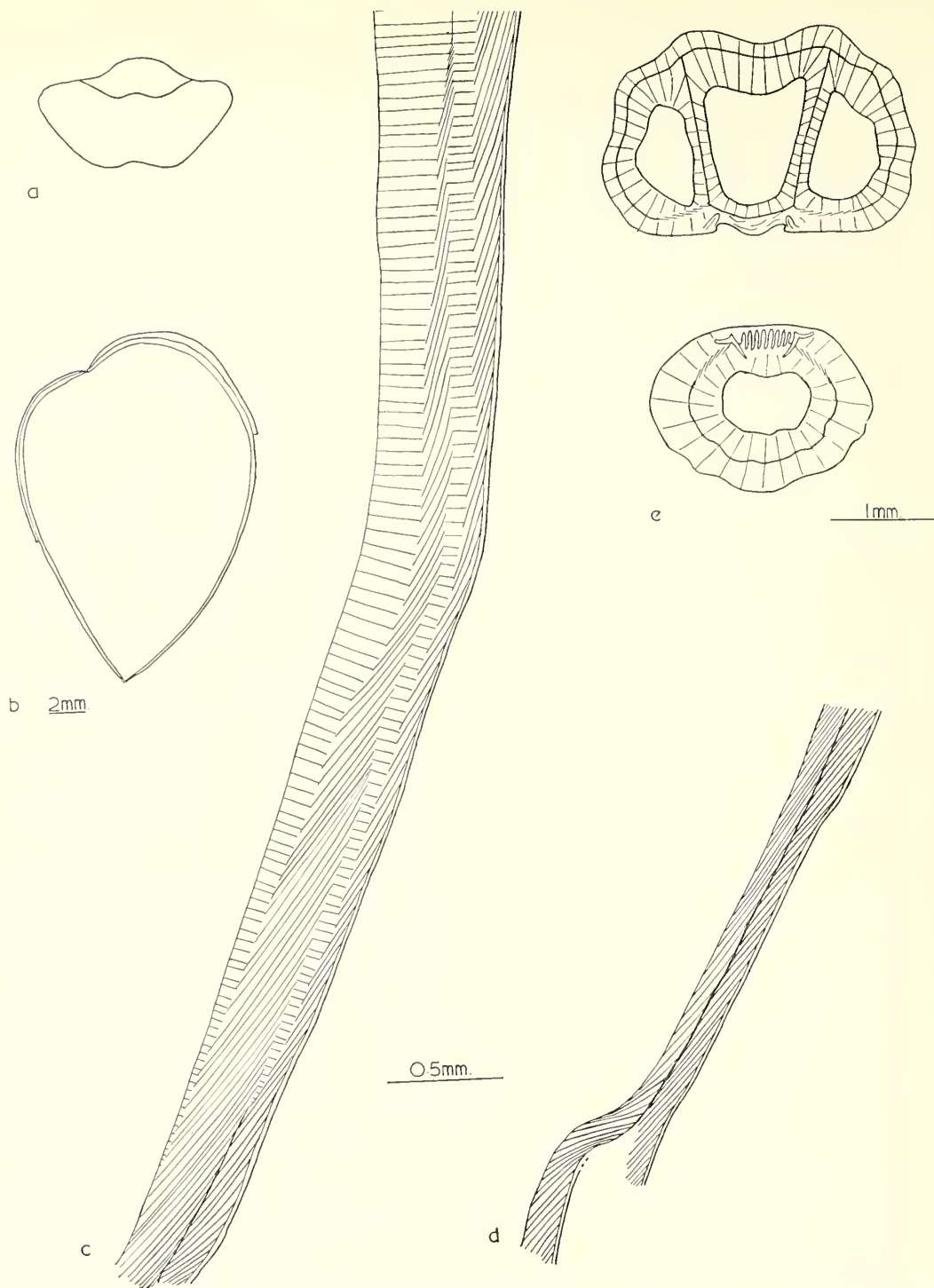
Mode of formation of fibrous and columnar layers. Since the columnar and fibrous layers differ in their structure and in their pattern of development it seems probable that they were deposited by different parts of the mantle. Williams (1956, p. 246) shows that the secondary (=fibrous) layer forms at the mantle edge and increases in thickness with growth. Its secretion is intracellular, each fibre having a corresponding epithelial cell. The columnar layer clearly did not form at the mantle edge, and the larger dimensions of its crystals indicate that the mantle secreting it was of a different form from that secreting the fibrous layer. Williams (1956, p. 250) considers that an inner layer of this type is formed by extracellular secretion.

The reason for the modification of the mantle posteriorly is not known. Though the columnar layer corresponds in area with the viscera it seems unlikely that there was any genetic relation between the viscera and the columnar layer since most brachiopods and many spiriferids are devoid of columnar layer.

The interlayering of the shell suggests that the same part of the mantle could secrete both types of shell material, yet the mantle secreting fibrous layer was apparently structurally different from that secreting columnar layer. To produce interlayering, the mantle would be required to change in structure repeatedly. The interlayering, however, only developed after a growth halt and the formation of fibrous layer on columnar layer



TEXT-FIG. 6. Interlayering of columnar and fibrous layers in the shell of *Spirifer trigonalis* (Martin). *a*, Longitudinal section showing two interlayerings of fibrous and columnar layers. *b*, Transverse section showing two 'lenticles' of columnar layer in fibrous layer. *c*, Transverse section showing several interlayerings (columnar layer black). *d*, Enlargement of part of fig. *c*, showing four fibrous and four columnar layers. *e*, Transverse section of ventral sulcus showing interdigitation of fibrous and columnar layers. *f*, Transverse section of dorsal fold of the same specimen as in fig. *e*, showing a corresponding development of 'lenticles' of columnar layer.



TEXT-FIG. 7. Modification of the shell of *Spirifer trigonalis* (Martin), due to a growth pause. *a*, External view showing one prominent growth-line. *b*, Longitudinal section of the same specimen showing the corresponding internal growth-line. *c*, *d*, Longitudinal section with detailed microstructure showing interlayering of fibrous and columnar layers, growth-lines in both columnar and fibrous layers, external growth-line, and interruption of lamellar layer. *e*, Transverse sections through the apices of both valves showing a growth-line in columnar layer and interlayered fibrous layer in the interareas.

would appear to result instead from a contraction of the mantle which brought that part of the mantle responsible for the secretion of fibrous layer over an area in which columnar layer had been deposited before the growth halt (text-fig. 8).

Since the secretion of the fibrous layer is intracellular a contraction of the mantle would have caused disruption of the epithelial cells. This is apparently borne out by the complete lack of correspondence of the fibres of the fibrous layer across the growth line (text-fig. 7*d*). In the columnar layer, on the other hand, there is continuity of crystal structure across the growth-lines, but this does not imply absence of mantle contraction since the prisms would develop in crystallographic continuity as long as secretion was extracellular.

The amount of contraction of the mantle would be variable depending probably on the duration of the growth pause. It is measured by the length of the zone of interlayering which it produced. The maximum observed is 5 mm. It is possible that greater contraction occurred, for the epithelial cells may be rendered incapable of further secretion and then the generative zone, close to the mantle edge, would have had to be brought back into the shell in a position corresponding to the posterior end of the inner oblique layer. This is an observed maximum of 8 mm.

INTERNAL MORPHOLOGY OF THE SHELL AND ITS DEVELOPMENT

Terminology of internal plates. *Median septum* (text-fig. 4*d*): any plate in the longitudinal, median plane of either valve is referred to as a median septum.

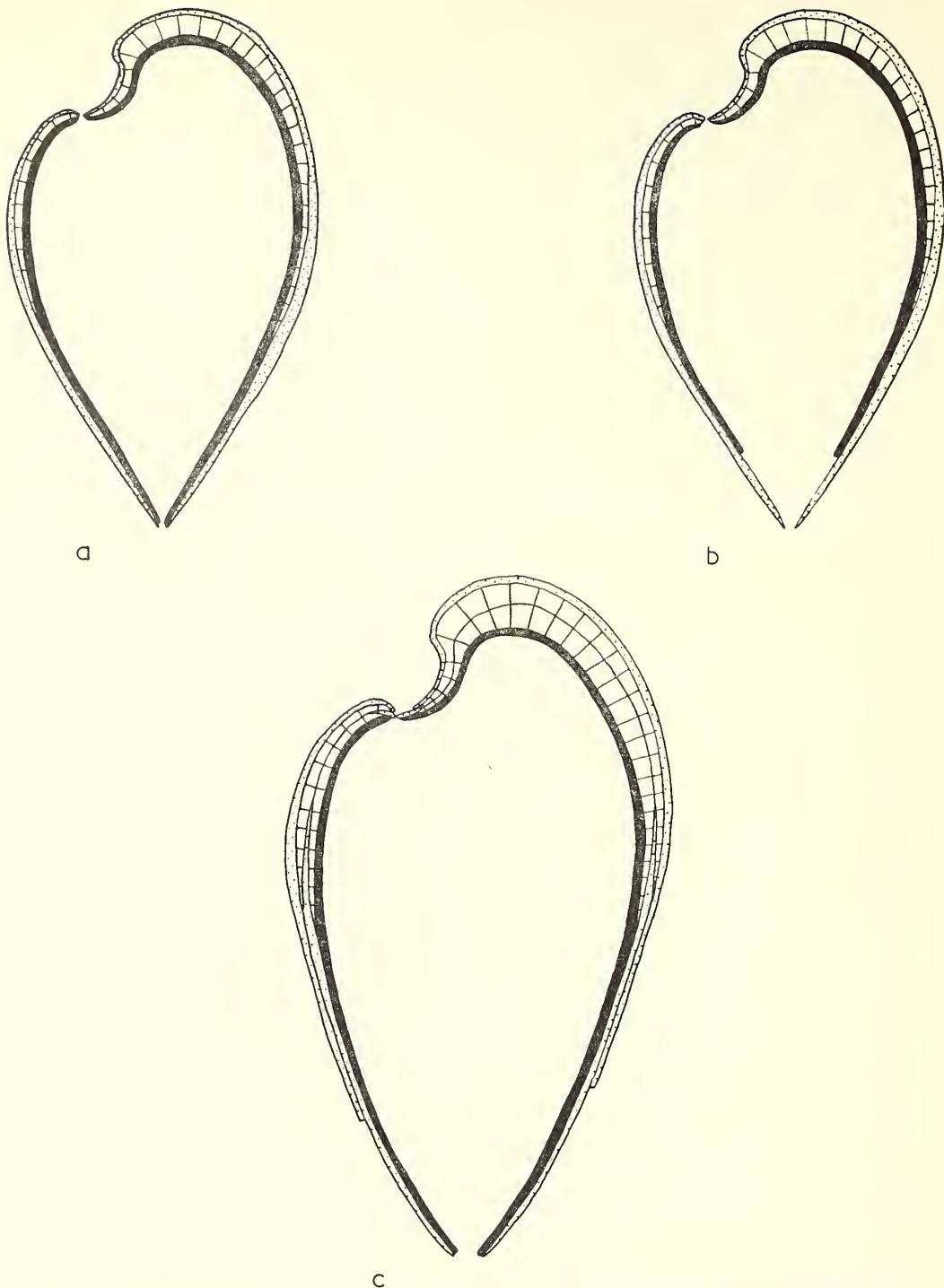
Dental plates (text-fig. 4*f*): this term, first used by King (1850, p. 68), refers to two vertical plates which project from the delthyrial margins, across the apical cavity, to the floor of the valve.

Dental ridge (text-fig. 4*e*): Alexander (1948, figs. 3*f* and 6*a*) refers to the ridge along the delthyrial margin in pentamerids as a dental ridge. The ridge represents the successive growth stages of the hinge tooth. Cooper (1954, p. 328) refers to the same structure in spiriferids as 'the growth track of the tooth'. Alexander's term is adopted here.

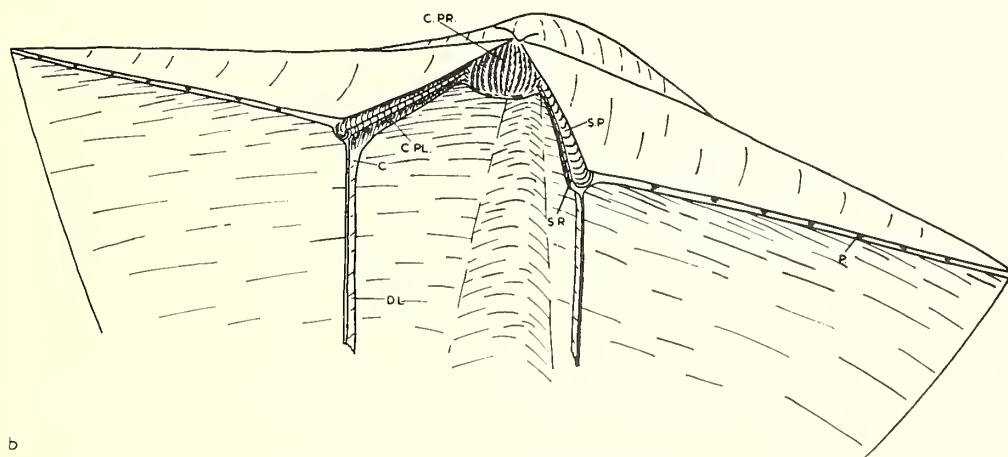
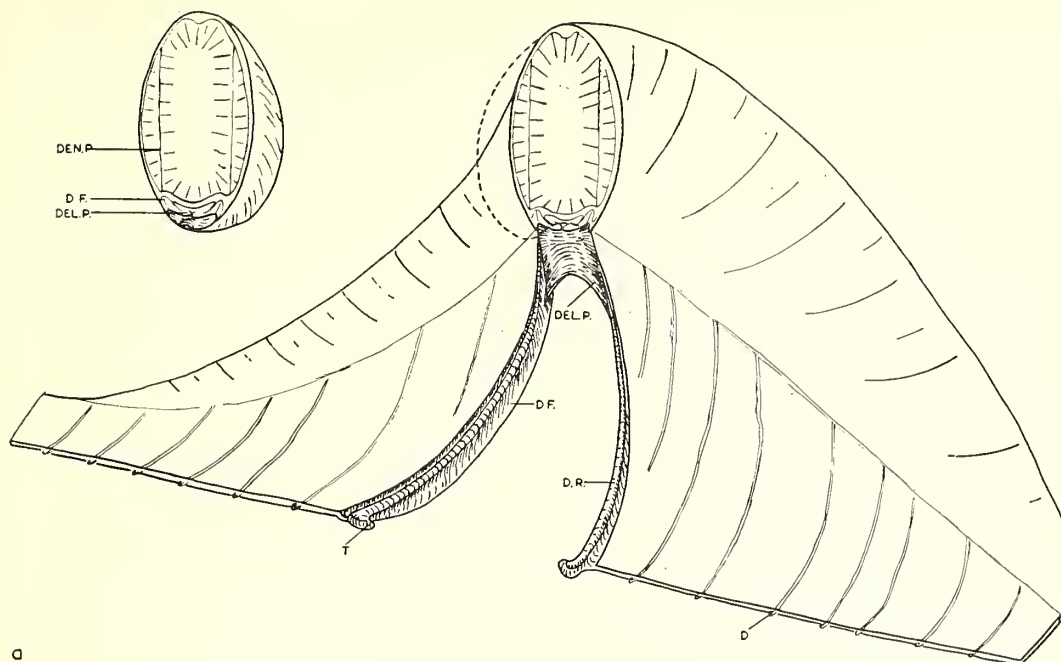
Dental flange (text-fig. 4*e*): this is a new term proposed for a subsidiary dental structure. The dental flange is a projecting plate on the inner side of the dental ridge. It extends along the length of the dental ridge and is directed into the delthyrial cavity, making an obtuse angle with the interarea. The two flanges, on either side of the delthyrium, are thus convergent. For part of its length the dental flange is buried within the dental plate (text-fig. 4*f*).

Delthyrial plate (text-fig. 4*g*): several terms have been used to describe the plate which extends across the delthyrium, between the dental plates, closing the delthyrium at the apex and extending anteriorly to a greater or less extent. Hall (1867, pp. 248 and 254) uses transverse septum, Hall and Clarke (1894, p. 29) use transverse plate, Cooper (1954, p. 328), Stainbrook (1943, p. 421), and Miloradovitsch (1937, fig. 16) use transverse delthyrial plate, Fredericks (1927, p. 3) simply uses delthyrial plate. Fredericks's term is adopted.

Methods of interpretation of development. Three lines of evidence are used in tracing the development of the internal structures of the shell. Firstly, direct evidence is derived from a comparison of young and old specimens. Secondly, the sequence of development



TEXT-FIG. 8. Hypothetical reconstruction of the mantle in *Spirifer trigonalis* (Martin). Mantle is shown in solid black. *a*, Shell before a growth halt with mantle in normal position. *b*, Shell during a growth halt with mantle retracted. *c*, Shell after a growth halt showing interlayering of the shell and readvance of mantle. (Approximately $\times 4$.)



TEXT-FIG. 9. Reconstruction of the apices of the valves of *Spirifer trigonalis* (Martin). *a*, Pedicle valve with umbo inset. *b*, Brachial valve. Abbreviations in this and subsequent text-figures: den. p., dental plate; del. p., delthyrial plate; d.f., dental flange; d.r., dental ridge; t., tooth; d., denticle; c., crus; c. pl., crural plate; c. pr., cardinal process; d.l., descending lamella; s.r., socket ridge; s.p., socket plate; p., pit.

can be proved in some parts of the shell where later structures are superimposed on early structures without any resorption of the previous shell substance. Thirdly, the shell layers show growth-lines which illustrate the form of particular parts of the shell at successive stages in growth.

The pedicle valve. The dental ridges and dental flanges lie along the delthyrial edges; the dental plates fall from the margins of the delthyrium to the floor of the valve where the median septum rises; the delthyrial plate, supported between the dental flanges, closes the delthyrium for about a quarter of its length (text-fig. 9a). Enveloping all these structures to some extent is the apical infilling, a development of columnar layer ('callus') on the inner surface of the umbo (text-fig. 9a inset).

The extreme apex of the valve is without dental ridges, flanges and plates (text-fig. 11o).

Thus, at the earliest stage which can be inferred, the pedicle valve was gently convex, with an open delthyrium, and was composed of lamellar layer and fibrous layer. With growth, the fibrous layer thickened away from the umbo, and, even at a young stage, was succeeded by columnar layer.

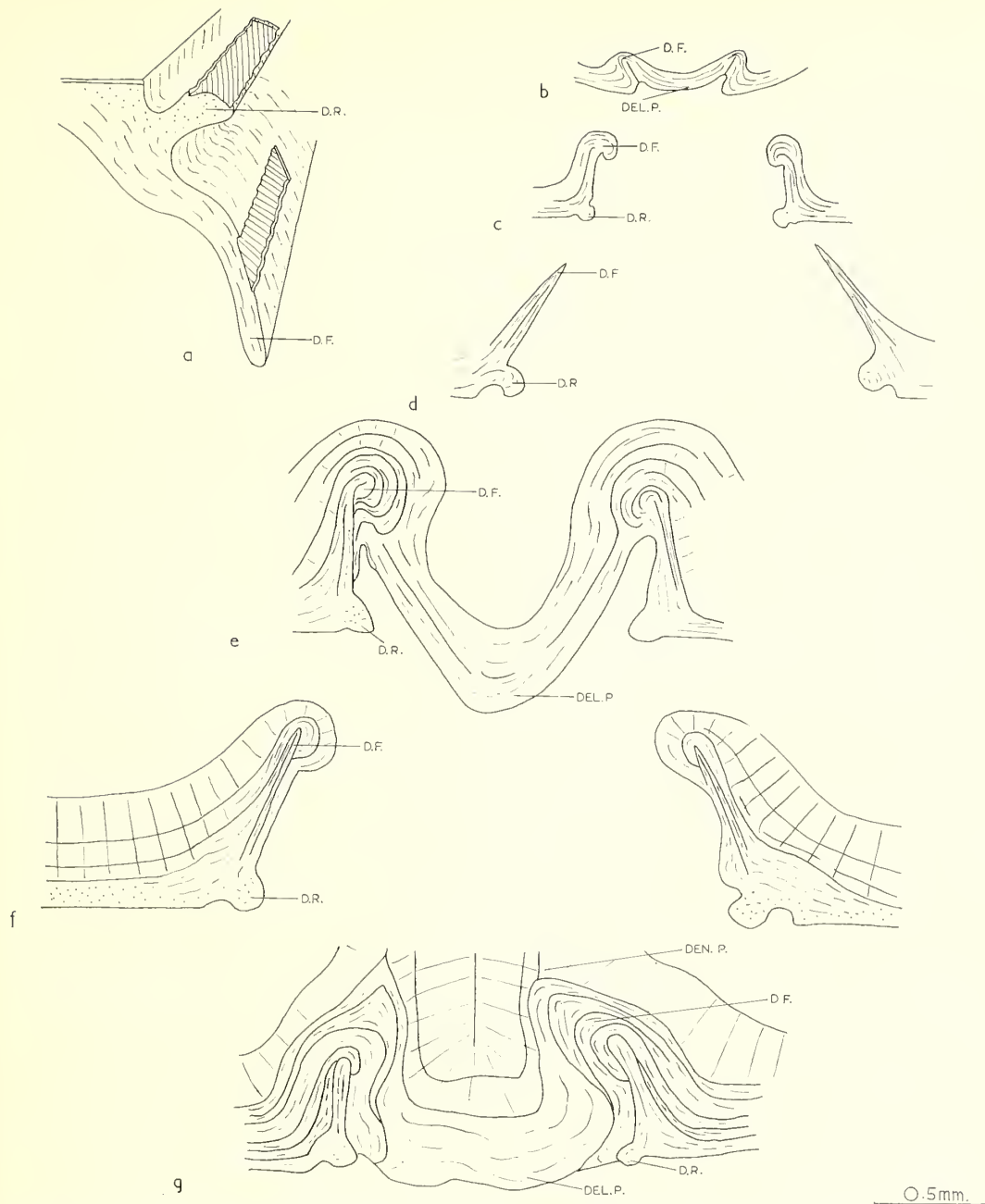
Dental ridges and dental flanges: the dental ridges appear about 0.5 mm. from the umbo (text-fig. 10c). Subcircular in transverse section, they increase in size anteriorly to a diameter of about 0.25 mm. They are separated from both the interarea and the dental flanges by grooves (text-fig. 10a). The dental flanges appear slightly posterior to the dental ridges (text-fig. 10b) and extend along the inner surface of the ridges. They increase in width to about 1 mm. close to the cardinal margin, before dying out just short of the teeth. Anteriorly the flange has an angular inner edge (text-fig. 10d), but as it is traced posteriorly its form changes, so that at mid-length the inner edge is curved over and a low ridge is formed on the outer surface of the flange (text-fig. 10c).

Both dental ridges and dental flanges are composed of fibrous layer and where flange and ridge come in contact the fibres are intergrown (text-fig. 10a). In the ridges the crystals lie normal to the hinge-line, and intersect the edges of the ridges. In the flanges a distinct median plane divides the fibrous layer into two sheets which merge along their inner edges. The fibres lie normal to the length of the flange and parallel to the median plane, never crossing it (text-fig. 10d).

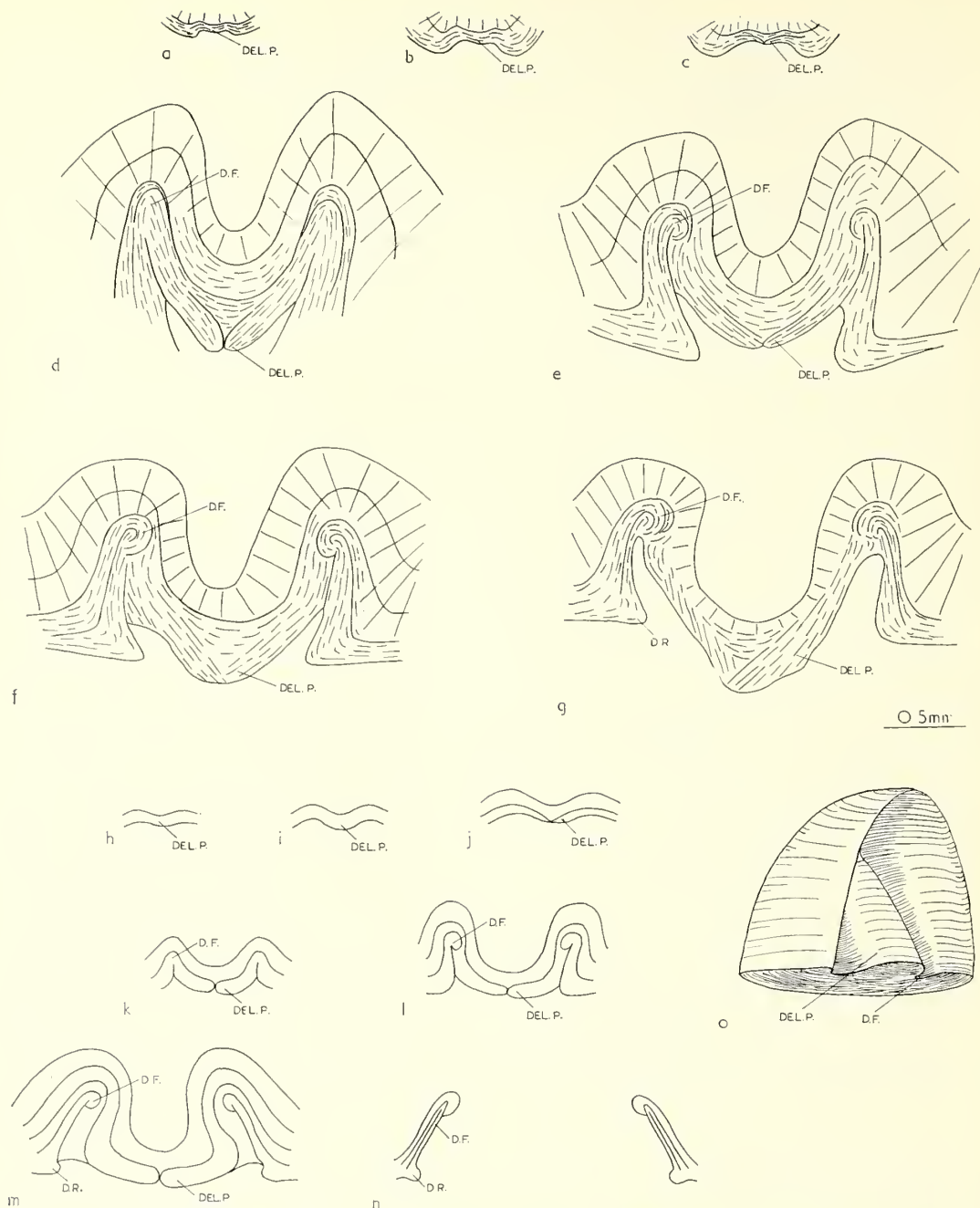
From the double structure of the dental flanges it is inferred that they, together with the dental ridges, were secreted by two small mantle folds bordering the delthyrium. The later development of the flanges is seen in the adult shell where several successive layers can be recognized in each flange. These are best developed on the inner surface where they consist in large part of columnar layer. The form of the flange, in some cases, was changed at this stage, a curved flange forming around a small angular-edged one (text-fig. 10f).

Delthyrial plate: throughout its length the delthyrial plate is convex, and anteriorly the convexity is sufficient to bring the plate above the level of the delthyrium (text-fig. 11g). Its free margin is concave. Columnar layer is present on the inner surface, but much of the plate is formed by fibrous layer, the fibres lying parallel to the surface and oblique to the length of the plate (text-fig. 11a-g).

Since the delthyrial plate consists only of fibrous and columnar layers, no lamellar layer extending on to it from the interarea, it is considered to be an internal structure which was covered by the mantle throughout life (cf. Williams 1953, p. 280). It would



TEXT-FIG. 10. Dental flanges and dental ridges in *Spirifer trigoualis* (Martin). *a*, Reconstruction of dental ridge and dental flange, dissected to show the orientation of the fibres ($\times 60$). *b-d*, Three transverse sections through apex of delthyrium. Section interval 0.05 mm. *b*, Dental flanges and delthyrial plate; *c*, *d*, dental flanges and dental ridges. *e-f*, Two transverse sections, 1.25 mm. apart. *e*, Multi-layered dental flanges with delthyrial plate and dental ridges; *f*, multi-layered dental flanges and dental ridges. *g*, Multi-layered dental flanges and delthyrial plate covered by bases of dental plates.



TEXT-FIG. 11. Delthyrial plate in *Spirifer trigonalis* (Martin). *a-g*, Transverse sections of the structures at the apex of the delthyrium, section interval *a-b*, 0.10 mm., *b-c*, 0.05 mm., *d-e*, 0.05 mm., *e-f*, 0.15 mm., *f-g*, 0.30 mm., showing development of delthyrial plate and emergence of dental flanges. *h-n*, Diagrammatic representation of development of delthyrial plate and dental flanges ($\times 20$). *o*, Reconstruction of umbo of pedicle valve showing delthyrial plate arising from floor of valve a short distance from umbo. (Approximately $\times 25$.)

have been formed within a mantle fold which rose from the floor of the valve a short distance from the umbo, crossed the apical cavity to the delthyrium, and bent back on itself to the floor of the valve (text-fig. 11o). In this way, not only would the delthyrial plate have been initiated, but the infilling of the apical cavity would also have begun. This mantle fold would be flanked by the two smaller folds in which the dental ridges and flanges would be secreted.

Apically the structure of the dental flanges merges with that of the delthyrial plate (text-fig. 10b), and at the summit of the delthyrium the flanges are rudimentary, not distinctly separable from the plate (text-fig. 11a, b). Initially then the delthyrial plate and its flanking dental flanges formed simultaneously (text-fig. 11h, i). But, anteriorly, a median parting of fibres develops in the outermost layer of the plate (text-fig. 11c, d, e, j, and k), minor discontinuities form laterally (text-fig. 11f), and finally the dental flanges appear as discrete structures from which the delthyrial plate is suspended (text-fig. 11l). It seems then that the lateral parts of the mantle fold grew in advance of the median part. Sometimes a considerable interval would elapse between the appearance of the dental flange and the secretion of the delthyrial plate, for there are several successive layers in the flange beneath the delthyrial plate (text-fig. 11m). Anteriorly the dental flanges completely outstrip the delthyrial plate and the anterior part of the delthyrium remains open (text-fig. 11n).

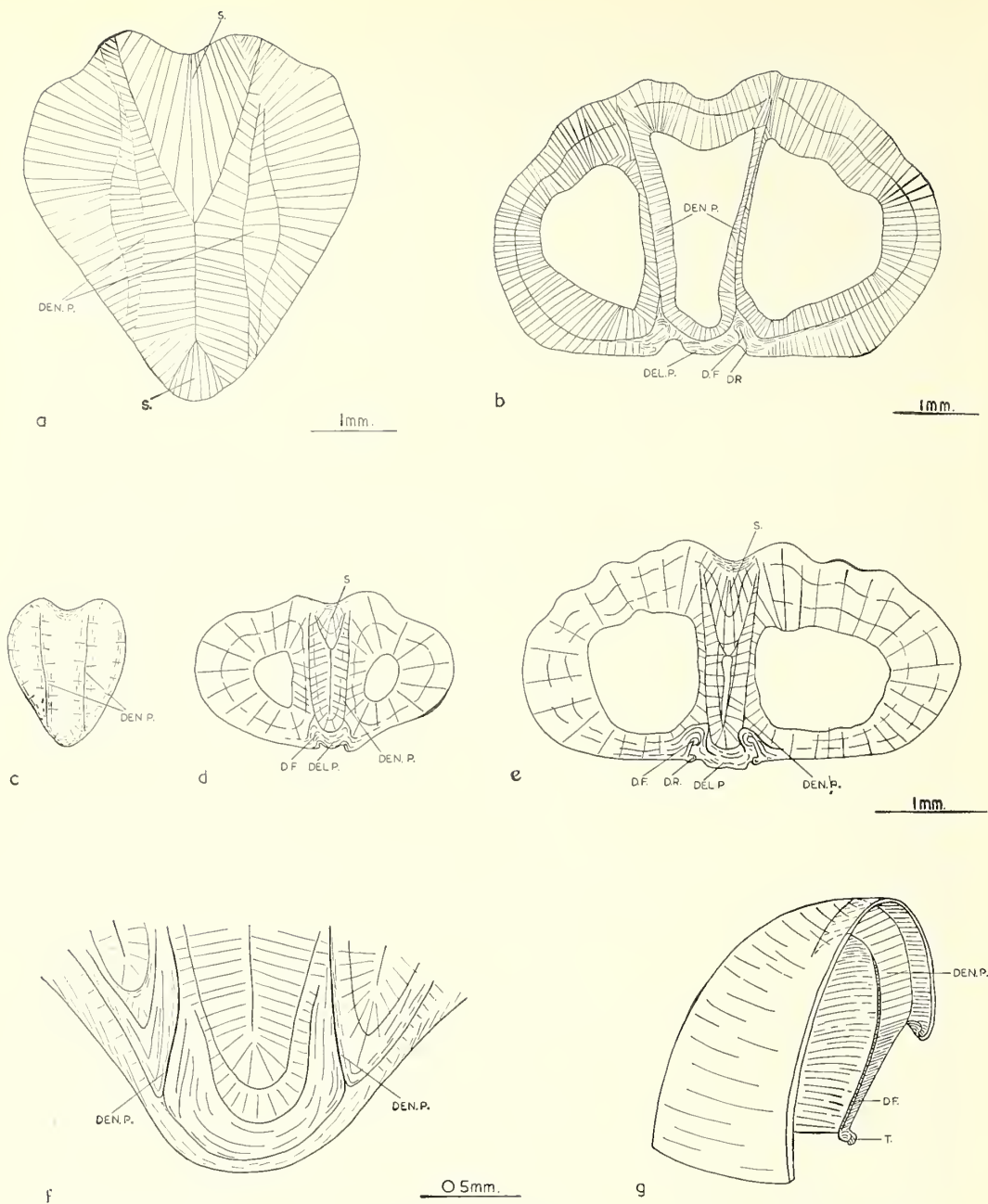
There is no indication that any secretion took place on the outer surface of the delthyrial plate after its formation, though it is assumed that it remained enveloped by mantle since no lamellar layer is present on it. The plate grew in thickness internally. This is in contrast to the dental flanges in which secretion continued on both outer and inner surfaces, though the inner growth greatly exceeds the outer.

Median septum: at approximately 0.5 mm. from the tip of the umbo a low, narrow, median ridge rises on the floor of the pedicle valve and extends for about a third of the length of the valve, widening anteriorly. Beneath the septum there are, in some cases, unfolded layers of the shell wall. It is thus inferred that, when the shell had become somewhat thickened, and while the structures just described were forming around the delthyrium, the median septum was secreted by a fold of the mantle on the floor of the valve.

Dental plates: the dental plates extend along the margins of the delthyrium, posteriorly from the teeth, but whereas the delthyrial margins converge, the dental plates become nearly parallel posteriorly and never reach the umbo (text-fig. 12c-e). They cross from the interarea to the floor of the valve some little distance anterior and lateral to the umbo (text-fig. 12g). Their position relative to the dental flanges is thus variable along their length (text-figs. 12b-e). They show much variation in length, but commonly extend a very short distance on the floor of the valve (text-fig. 12g).

The dental plates are formed almost entirely of columnar layer. Each plate is made up of two parts, the surface separating the parts appearing in section as a well-defined line (text-fig. 12b). The crystals do not cross this line, usually meeting it at an angle. It is deduced from their double structure that the dental plates were formed within two parallel longitudinal invaginations of the mantle which extended from the delthyrium across the apical cavity to the floor of the valve, each side of a plate being formed by secretion from one side of a fold.

The two dental plates divide the apex of the valve into three chambers, a central



TEXT-FIG. 12. Dental plates in *Spirifer trigonalis* (Martin). *a*, Section through the incurved umbo passing twice through the septum. The dental plates, completely filling the umbo, are in contact with the septum. *b*, Transverse section showing the dental plates forming the apical cavities and enveloping the dental flanges. *c-e*, Three transverse sections, section interval *c-d*, 1.2 mm., *d-e*, 0.8 mm., showing the parallelism of the dental plates and their variable position relative to the dental flanges. *f*, Transverse section in the apex of the pedicle valve showing the thin shell layer external to the base of the dental plates. *g*, Reconstruction of the apex of the pedicle valve illustrating the parallelism of the dental plates posteriorly, their divergence along the delthyrial margin, and absence at the umbo. (Approximately $\times 5$.)

delthyrial cavity and two lateral umbonal cavities. Each cavity is lined with columnar layer which passes with slight discordance into the columnar layer of the dental plates (text-fig. 12*b, d, e*). The columnar layer in these cavities may be so thick apically that it fills the cavity; the dental plates are only recognized by the trace of the line of junction in each plate (text-fig. 12*c*) and the median septum is represented by a triangular wedge between the plates (text-fig. 12*a*).

The formation of the dental plates occurred after the thickening of the shell had proceeded to some extent, for the bases of the dental plates do not extend to the outer shell layers (Pl. 65, fig. 4; text-fig. 12*f*). In some cases the dental plates formed simultaneously with the median septum for growth-lines can be traced from the dental plate round the delthyrial cavity and across the septum (text-fig. 12*e*). In other cases the dental plates developed after the septum and completely enveloped it.

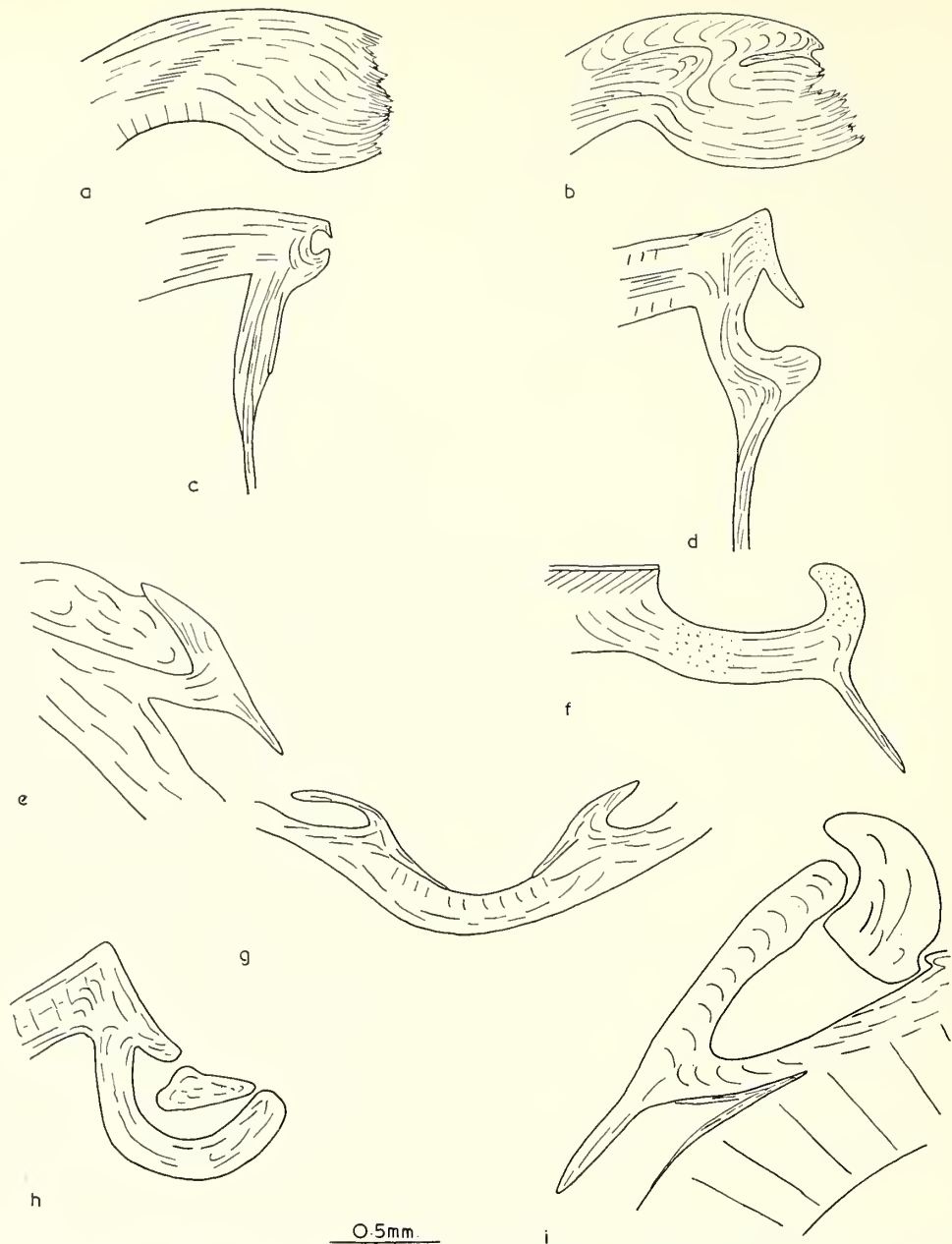
Further information about the stage at which the dental plates developed is obtained from young specimens. These possess dental ridges, dental flanges, and a delthyrial plate but are devoid of dental plates, showing that the dental plates developed later than these other structures. The same conclusion can also be drawn from the way that the dental plates grow over the dental flanges. Indeed it might seem that the dental flange was no more than an immature dental plate which was not long enough to reach the floor of the valve, but grew later into a full dental plate. However, this is not so, for the dental plates and dental flanges do not always correspond exactly in position, the delthyrial margins converging, and the dental plates remaining almost parallel (text-fig. 12*c-e*). The dental plates appeared as a new element in the ephebic shell; they did not develop out of a structure present in the neanic stages.

In at least one specimen the development of the dental plates took place immediately after a growth halt. The interruption in growth is recorded in the columnar layer of the apical chamber as a prominent growth-line. The dental plates are in continuity with the columnar layer within the growth-line, showing that the plates were secreted after the interruption of growth (text-fig. 12*b*).

At their youngest observed stage the dental plates form two relatively long ridges which extend from the delthyrium to the floor of the valve across the apex of the valve. At this stage they are not partitions, only low ridges. They are of uniform height suggesting that growth commenced simultaneously along their length, rather than extending gradually from a point. The position of the new dental plates in relation to the delthyrium corresponds with the position of the dental flanges immediately anterior to the delthyrial plate. The invaginations of the mantle in which the dental plates were secreted apparently formed in continuity with the mantle folds surrounding the dental flanges, where these became free from the delthyrial plate. Indeed, in their anterior prolongations the dental plates splay out along the delthyrial margins and are inseparable from the dental flanges.

As growth proceeded the low ridges of the dental plates developed into complete partitions in the apical cavity; they increased in thickness as the valve wall increased, till together they formed the apical infilling; and, as the dental flanges became thicker and the delthyrial plate grew anteriorly between them, the dental plates too extended anteriorly, growing around the dental flanges and resting on the delthyrial plate with their bases between the dental flanges.

The material infilling the umbo, essentially columnar layer, is commonly referred to as the 'umbonal callus' and dismissed as a late-stage infilling of no great significance.



TEXT-FIG. 13. Dental sockets in *Spirifer trigonalis* (Martin). *a-d*, Four longitudinal sections through the cardinal process and dental sockets. Section interval, *a-b*, 0.1 mm., *b-c*, 0.6 mm., *c-d*, 0.4 mm. *a*, Sagittal section showing irregular surface of cardinal process; *b*, early formed dental socket and crus within cardinal process; *c*, dental socket and crus emerging from cardinal process; *d*, dental socket with overhanging interarea and descending lamella attached to convex surface. *e*, Transverse section showing dental socket infilled by later material. *f*, Transverse section of dental socket with well-developed socket ridge and crural plate attached to convex surface of socket. *g*, Transverse section showing crural plates fused to the floor of the valve. *h*, Tooth and socket in longitudinal section. *i*, Tooth and socket in transverse section.

The apical infilling, intimately connected with the dental plates and other delthyrial structures, is as much a part of the shell as the outer layers, and it is to be regarded as reflecting a stage in the formation of the shell no less important than that preceding it.

The brachial valve. At the earliest growth stage which can be inferred, the brachial valve like the pedicle valve was formed of lamellar layer and fibrous layer and was without internal plates. As growth proceeded the fibrous layer became thicker, and at the umbo the formation of the cardinalia was initiated.

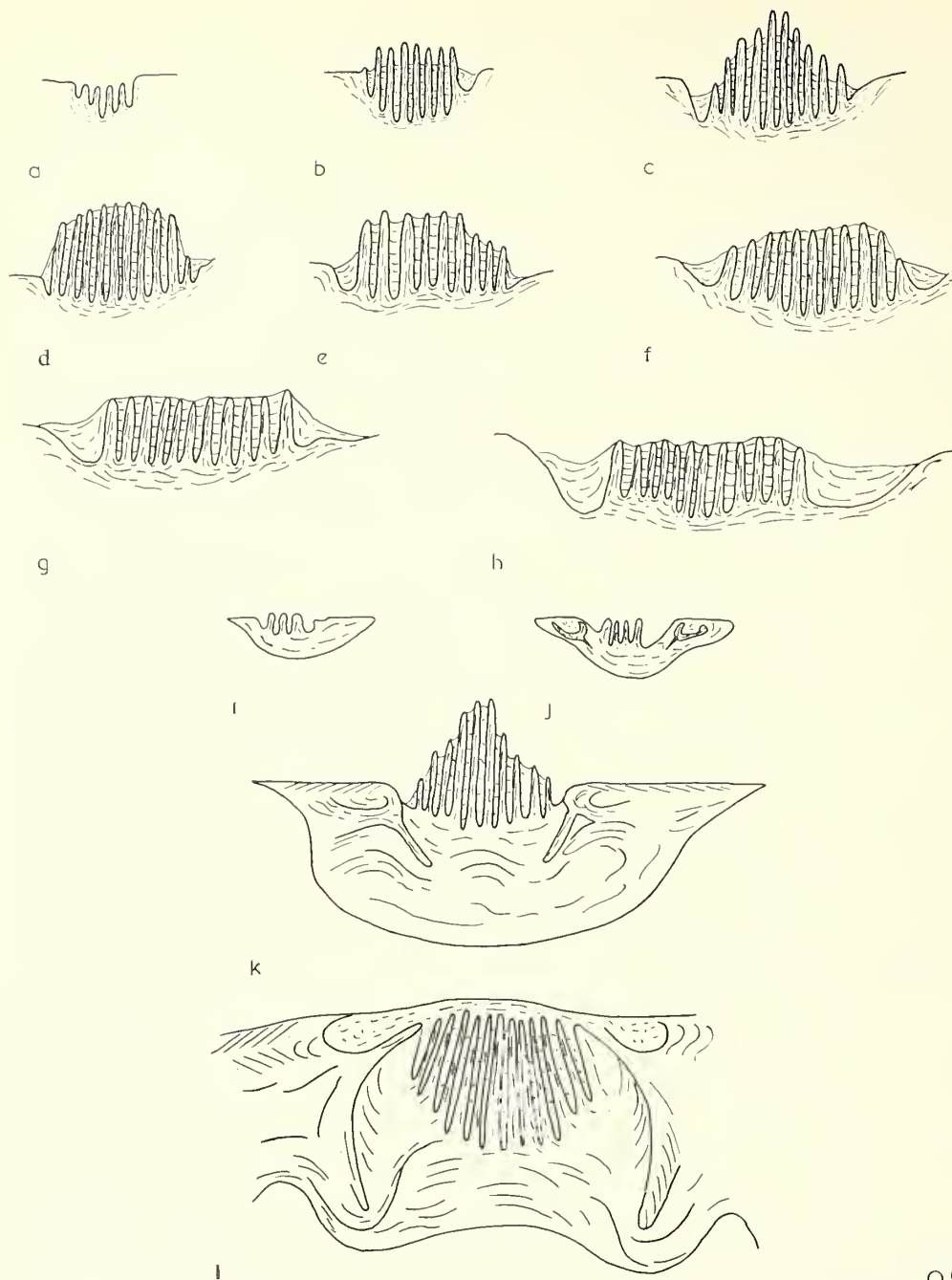
Dental sockets: the curved plates of the dental sockets extend along the inner margins of the notothyrium from about 0.1 mm. from the umbo to the hinge-line and project a little into the pedicle valve (text-fig. 9b). The sockets are larger and deeper anteriorly (text-fig. 13b-d) and their inner edges are turned up to form inner socket ridges (text-fig. 13f). The overhanging edge of the interarea functions as an outer socket ridge (text-fig. 13d). Both the sockets and the interarea are formed by fibrous layer but the structure of each is distinct: the fibres in the interarea lie along its width, inclined inwards, away from the notothyrium; those in the socket lie in the longitudinal plane and curve around the socket (text-fig. 13d, f).

Crura and crural plates: the crura are attached along the convex under surface of the dental sockets (text-fig. 13d). Their descending lamellae, about 0.75 mm. in width, parallel with the notothyrial margins, extend almost to the anterior margin before rotating into a plane parallel with the width of the shell and giving rise to the spiralia. The crural plates extend along the length of the dental sockets and anteriorly are continuous with the crura (text-fig. 9b). They increase in width anteriorly from 0.3 mm. to 1.3 mm. and, due to the spiral growth of the shell, change in inclination along their length through an angle of about 90° (text-fig. 13b-d). It is inferred that the dental sockets and crural plates were secreted by two mantle folds extending along the notothyrium; and the crura and spires, formed in structural continuity with the dental sockets, were secreted by two offshoots of the mantle folds. There is no indication of successive layers within the socket or crural plates, so they did not increase in thickness with growth. As the socket plates extended during the growth of the shell, the early sockets were abandoned, and were later infilled.

The earlier-formed descending lamellae of the crura are not preserved and there is no trace of any but the latest stage in the development of the spires. It is concluded that the spires and descending lamellae were continually resorbed and grown again; only the crural bases remain intact, later enveloped in the cardinal process.

Cardinal process: the cardinal process is of the striate type usual in spiriferids (text-fig. 9b). It is situated at the apex of the notothyrium and spreads laterally to envelop the posterior parts of the socket and crural plates (text-figs. 13a, 14k). The earliest-formed part of the cardinal process is at the apex of the notothyrium, where no dental sockets are present (text-fig. 14i). It may therefore have been formed earlier than the sockets, but it is more probable that it was formed at the same time as the sockets though slightly posterior to them.

It is composed entirely of fibrous layer, the dorso-ventrally elongate fibres giving rise to a smooth lower surface and an irregular upper surface where the ends of the fibres are free (text-fig. 13a). This upper surface is the area of muscle attachment. The fibres are in continuity with those of the fibrous layer of the shell wall, only a flexure of the fibres



0.5mm

TEXT-FIG. 14. Cardinal process in *Spirifer trigonalis* (Martin). *a-h*, Series of transverse sections, section intervals *a-b*, 0.12 mm., *b-c*, 0.08 mm., *c-d*, 0.05 mm., *d-e*, 0.05 mm., *e-f*, 0.05 mm., *f-g*, 0.10 mm., *g-h*, 0.03 mm., showing the anterior increase in number of plates in cardinal process. *i-j*, Transverse sections through the cardinal process of a young individual. *k*, Cardinal process and flanking dental sockets and crural plates attached to the valve floor by later shell growth. *l*, Stages in the envelopment of the crural plates shown by growth-lines. The dental sockets and grooves in the cardinal process both infilled.

defining the process (text-fig. 13*b*). It is inferred that the cardinal process was secreted by a fold of the mantle which rose from the floor of the valve near the umbo, extended across to the notothyrium, and then folded back to the floor of the valve. There is thus an analogy to be drawn between the development of the socket plates, crural plates, and cardinal process on the one hand, and the dental ridges, dental flanges, and delthyrial plate on the other.

The fibres are arranged in a series of vertical plates which extend through the substance of the process, but are themselves enveloped in fibrous calcite which leaves only the ends of the plates exposed as ridges on the area of muscle attachment (text-fig. 14*a-h*). The plates, two or three in number posteriorly, increase anteriorly to about fourteen, the median plates projecting above the level of the interarea.

As growth proceeded, then, the cardinal process was widened by the addition of extra plates and deepened by the elongation of the plates, and as it grew it encroached on the dental sockets, wrapping round them and burying the crural plates (text-fig. 13*b, c*). The material infilling the obsolete dental sockets is in continuity with that filling the spaces between the plates of the cardinal process (text-fig. 14/) so it is inferred that, at the same time as the cardinal process was growing laterally, the mantle would be retreating from the deeper parts of the grooves of the cardinal process, leaving behind a deposit of fibrous calcite, and thus keeping the grooves relatively shallow in spite of the elongation of the plates.

Articulation of the valves. The articulation provided by the teeth and sockets is highly effective, for not only is the tip of the tooth curved to fit into the socket but there are also two concave surfaces on the tooth on which rest the socket ridges (text-fig. 13*i*).

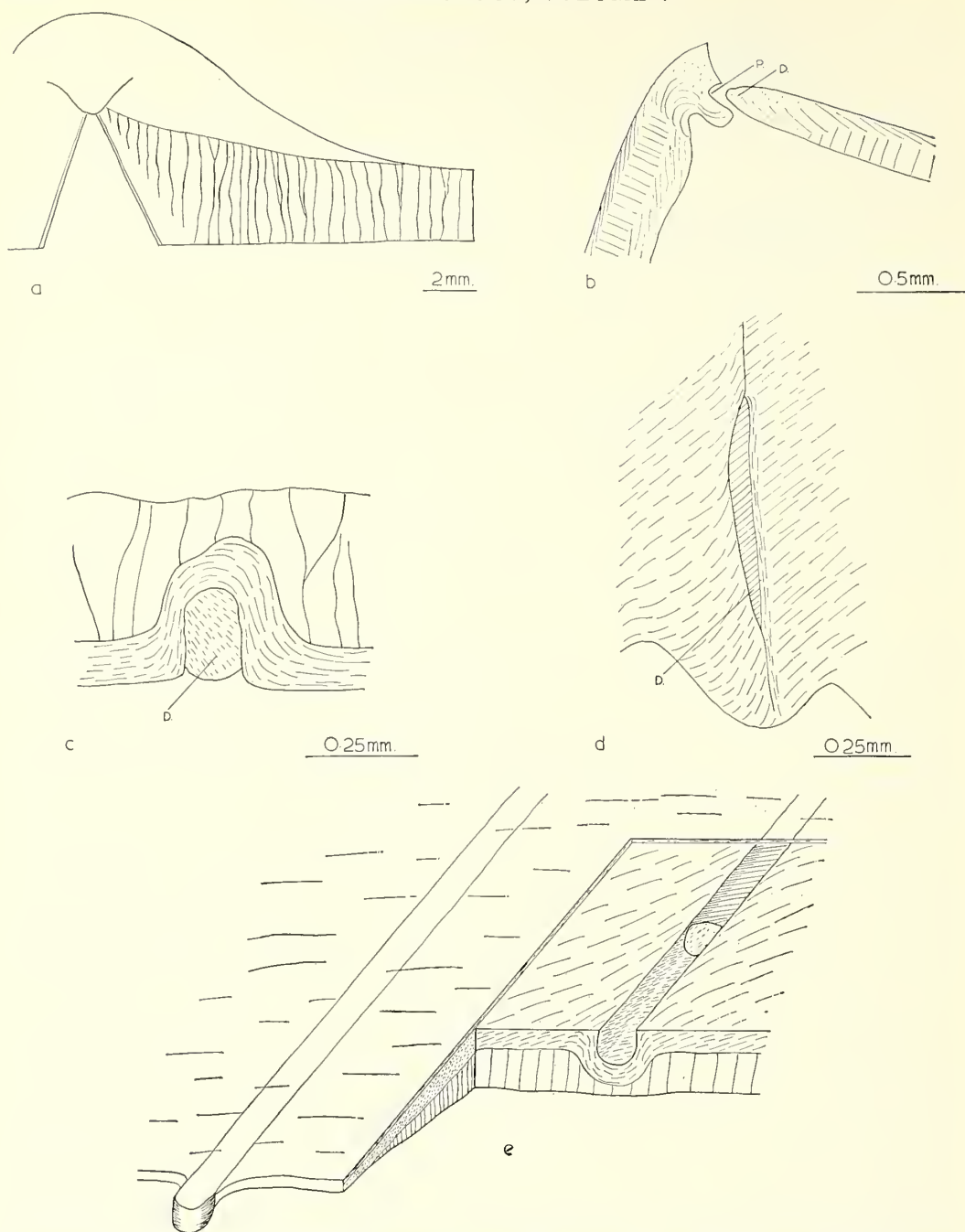
Denticles and pits: along the edges of the interareas of the wide shell there is a series of pits and denticles which provide an additional articulation. The denticles are in the pedicle valve and the pits in the brachial valve (text-fig. 9). In a specimen 35 mm. wide there are about twenty-five on each side of the delthyrium.

The denticles are normally hidden, but a series of subparallel, slightly sinuous, irregularly spaced, vertical striations are usually visible on the ventral interarea (text-fig. 15*a*). The striations are the grooves produced by the weathering out of the denticle tracks, and, on a well-preserved specimen, with lamellar layer intact on the interarea, no striations are visible (text-fig. 15*e*). The striations are absent from a narrow band on either side of the delthyrium (Pl. 64, fig. 26, text-fig. 15*a*).

Yanishevsky (1935) considered that the striations represent canals just below the surface; and Young (1884) thought the structures were composed of recrystallized aragonite, but the denticle tracks are no different in micro-structure from the rest of the shell (text-fig. 15*b*). They consist of bundles of fibres extending posteriorly from each denticle, distinct from the fibrous layer of the rest of the interarea only in the arrangement of the fibres (text-fig. 15*c, d*). The denticle tracks lie immediately below the lamellar layer and are covered on the underside by the fibrous and columnar layers of the interarea (text-fig. 15*e*).

The pits are negative features formed by the undulations of the fibres of the fibrous layer of the dorsal interarea.

The denticles would grow by the progressive elongation of the bundles of fibres, and as they advanced the lamellar layer grew anteriorly to cover their tracks, while the



TEXT-FIG. 15. Denticles and pits in *Spirifer trigonalis* (Martin). *a*, Ventral interarea with sinuous denticle tracks, occasionally fusing. Area with no denticle tracks bordering delthyrium. *b*, Longitudinal section of denticle in pit. *c*, Transverse section of denticle enclosed in fibrous and columnar layers of the interarea. *d*, Longitudinal section of denticle enclosed in fibrous layer of the interarea. *e*, Reconstruction of the ventral interarea showing the orientation of fibres in the denticle and in the interarea and the thinning of the columnar layer anteriorly.

fibrous layer enveloped them on the inner side. At a later stage columnar layer was formed. New denticles were added at the extremities as the hinge elongated, while a few were suppressed by the widening of the delthyrium. Occasionally two adjacent denticles merged to form one. The denticles projecting into the brachial valve would cause undulations of the mantle and in these depressions the pits would develop.

My thanks are due to Professor T. Neville George for supervision of the research, and for the help and encouragement he has given to me in this work.

I also thank Dr. Helen Muir-Wood for giving me access to specimens in the British Museum (Natural History) and for her kindly advice; and Mr. R. B. Wilson for allowing me to examine material in the Geological Survey collections at Edinburgh.

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A REVIEW OF THE EVIDENCE FOR A 'NEBRASKAN' FAUNA IN THE SCOTTISH CARBONIFEROUS

by R. B. WILSON

ABSTRACT. W. Hind claimed that a lamellibranch and gastropod fauna from the lower part of the Passage Group, Upper Carboniferous of Scotland, had strong North American affinities. The specimens on which this claim was based have been re-examined and it is now thought that this fauna is indigenous to Britain. Those specimens which can be identified specifically belong to species unrecorded from America. Two new lamellibranch species, *Euchondria bilstonensis* and *Schizodus taiti*, are described.

ABOUT the start of this century, palaeontological zoning of the Scottish Carboniferous succession was being attempted, based on plant and fish remains. The researches of Kidston and Traquair appeared to reveal a division into Lower and Upper Carboniferous, the break in the flora occurring about one-third of the way up the Scottish 'Millstone Grit'. D. Tait, a Geological Survey collector, while engaged in collecting plant specimens for Kidston, discovered several marine bands containing a rich molluscan fauna near the base of the 'Millstone Grit'. When the specimens were examined by Hind (1908, p. 332), he claimed that quite 50 per cent. of the lamellibranch species were new to Europe but bore a close resemblance to those found in the Coal Measures of Nebraska and Illinois. This conclusion had a profound effect on subsequent work on the zoning of the Scottish Carboniferous and has been quoted in most works on the subject. Confusion arose because, although Hind (op. cit.) stated that the fauna came from beds below the break between Lower and Upper Carboniferous floras, he also said that some members of the fauna resembled American Upper Carboniferous species and showed a marked approach to Permian types. The study of the goniatites by Currie (1954) has now placed the zoning of the Scottish Carboniferous on a much sounder footing. The present work is an attempt to re-examine the evidence which led Hind to describe what has become known as the 'Nebraskan Fauna' in Scottish Carboniferous literature.

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STRATIGRAPHY

When Hind (1908) described the Scottish fauna which he thought had close affinities with North American forms, only meagre knowledge existed of the strata from which the specimens had been collected. Several localities were involved, all of them in the Central Coalfield area except one in the Bilston Burn, Midlothian. For detailed accounts of the successions concerned, reference should be made to Francis (1956), Tulloch and Walton (1958), Read (1959), and Forsyth (1961). It is now known that the Limestone Coal Group is the lowest Upper Carboniferous formation in the Scottish Midland

Valley, as Currie (1954, p. 535) assigned a Lower *Eumorphoceras*, E_1 (basal Namurian) age to the Group. It is succeeded by the Upper Limestone Group, of Upper *Eumorphoceras*, E_2 , age, and Currie (op. cit.) also recorded E_2 goniatites from the basal marine band of the succeeding group, which was formerly called the Millstone Grit (of Scotland) but is now known as the Passage Group (MacGregor 1960). This latter formation is transitional between the Upper Limestone Group, which contains numerous marine bands, and the Coal Measures, which is mainly of non-marine origin. In the lower part of the Passage Group, rich marine faunas occur in limestones and mudstones but the upper and major part is mainly composed of sandstones and seat-clays with a few poorly fossiliferous shales usually containing only *Lingula*. The fauna under discussion came from the marine bands in the lower part of the Passage Group. Although goniatite evidence of an E_2 age has only been obtained so far from the lowest of these bands, the same molluscan fauna occurs throughout, and there is no reason to suppose that any great time interval separated the deposition of the lowest and highest bands. The maximum vertical distance separating them is 400 feet and there is no evidence of a major break within the strata containing the marine bands. The age of the fauna then is E_2 in the goniatite zonal scheme of the Namurian.

SPECIMENS FIGURED BY HIND

The Scottish specimens figured by Hind (1908, pls. 1, 2, figs. 1–58) have all been examined and the present writer's determinations and comments on the specimens are given below, the order being that in which Hind illustrated the material. Hind's identification is given first followed by the reference to his illustration. The specimens are housed in the Geological Survey Office, Edinburgh.

Lamellibranchs. Palaeolina retifera (Shumard), pl. 1, fig. 1. The specimen Hind figured, GSE 6436, was from a bed of shale in the pit shaft, Fireclay Works, Castlecary. It is an internal mould of a right valve with the anterior ear preserved, but the posterior ear is missing and the whole posterior end of the shell is crumpled and incomplete, giving a false outline. The specimen is refigured (Plate 66, fig. 1) but the orientation differs from that adopted by Hind. It is claimed that in Hind's illustration the hinge-line is turned through about 30 degrees in a clockwise direction from horizontal, giving the valve the appearance of having a produced posterior end.

This fossil is known from marine bands near the base of the Passage Group from several localities in the Central Coalfield and Midlothian. No well-preserved specimens have been found, but they bear a strong resemblance to *Palaeolina simplex* (Phillips) and, for the present, are best referred to as *P. cf. simplex*. The valve shape is quite different from that of *P. retifera*, the American species as illustrated by Meek (*in* Hayden 1872, pl. 9, fig. 5a). The most obvious difference is the absence of the markedly produced posterior end.

Aviculopecten regularis Hind, pl. 1, figs. 2, 3. Hind had two specimens available when he described this species, GSE 6420 (fig. 2) and GSE 6419 (fig. 3). They came from the marine band, found by D. Tait, 27 to 30 feet above the Castlecary Limestone (top of the Upper Limestone Group) on the right bank of the Bilston Burn, Midlothian. The exact locality is 220 yards S. 30° W. of the south-west corner of Bilston Lodge, near

Polton, and for convenience of reference it is here called the Polton Marine Band. Neither of the two syntypes quoted above is well preserved, but the left valve, GSE 6419, refigured on Plate 66, fig. 3, is here designated the lectotype. Subsequent collections made from the locality have yielded further specimens, but none is well preserved. Three of these are figured (Plate 66, figs. 5–7) to illustrate the species. The original description (Hind 1908, p. 341) is confirmed. The better material now available shows that the valves are acline or slightly prosocline, the costae on the almost flat right valve are more prominent than they appear on the poorly preserved right valve available to Hind, and the anterior ear of the right valve is quadrate in outline with a deep byssal notch separating it from the body of the valve. Hind did not claim American affinities for this species.

? *Aviculopecten neglectus* (Geinitz), pl. 1, figs. 4–7. Hind (1908, pp. 341–2) doubtfully referred some shells from the Polton Marine Band, Bilston Burn, to *Aviculopecten neglectus*. This is an American form which was designated the type species of the genus *Euchondria* Meek 1874 by Newell (1938, p. 104). Newell (op. cit., pl. 19, figs. 1, 4) illustrated the left valve of *Euchondria neglecta* showing that it is different from the Scottish form which is also a *Euchondria* and is described below as *Euchondria bilstonensis* sp. nov. (Plate 66, figs. 8–10).

Aviculopecten obliquus Hind, pl. 1, fig. 8. Hind (1908, p. 340) described this species from the previous locality. Confusion exists as to which specimen Hind actually illustrated. He stated that the figured specimen was numbered T4507b and was a right valve. The specimen numbered thus, now GSE 6417 (Plate 66, fig. 12), is the counterpart of GSE 6418 (Plate 66, fig. 11) which is a left valve, and Hind in fact shows a left valve although he stated that only right valves were present. GSE 6418 is almost certainly the specimen he used to illustrate the species and it is here designated the lectotype.

Subsequent collections from the locality have yielded eleven more specimens of this species, all left valves but one, none of which is complete. These specimens have confirmed Hind's diagnosis but to his description of the costae as nodulose should be added the fact that the nodes bear spines. These spines are seldom preserved, but they have been seen on several specimens, small ones being present on GSE 11892 (Plate 66, fig. 14) on the anterior margin. Also, a few costae are present on both anterior and posterior ears. This species is now placed in the genus *Pterinopectinella* Newell 1938 because of the presence of the spinose costae. It is much smaller and more prosocline than other described British species of *Pterinopectinella*. Hind did not claim American affinities for this form.

Limatulina alternata (M'Coy), pl. 1, figs. 9, 10. The specimens figured by Hind, GSE 6428–9, are poorly preserved, the latter having been crushed laterally, giving it a gibbose, narrow appearance. Newell (1938, p. 63) considered the generic name *Limatulina* to be a junior synonym of *Aviculopecten*. These specimens are not *Aviculopecten* and for the present are identified as '*Limatulina*' *alternata*. As Hind did not claim American affinities for this species it can be ignored here.

Pterinopecten whitei (Meek), pl. 1, figs. 11–13. Of the three specimens Hind figured, GSE 6450–2, only the last one is worth commenting on, as the other two are very poorly preserved and indeterminate. The specimen GSE 6452, now refigured (Plate 66, fig. 15), is from 40 feet above the Castlecary Limestone in the River Avon on the east side of the railway viaduct, 2 miles north of Linlithgow. It is an acline right valve with the margin

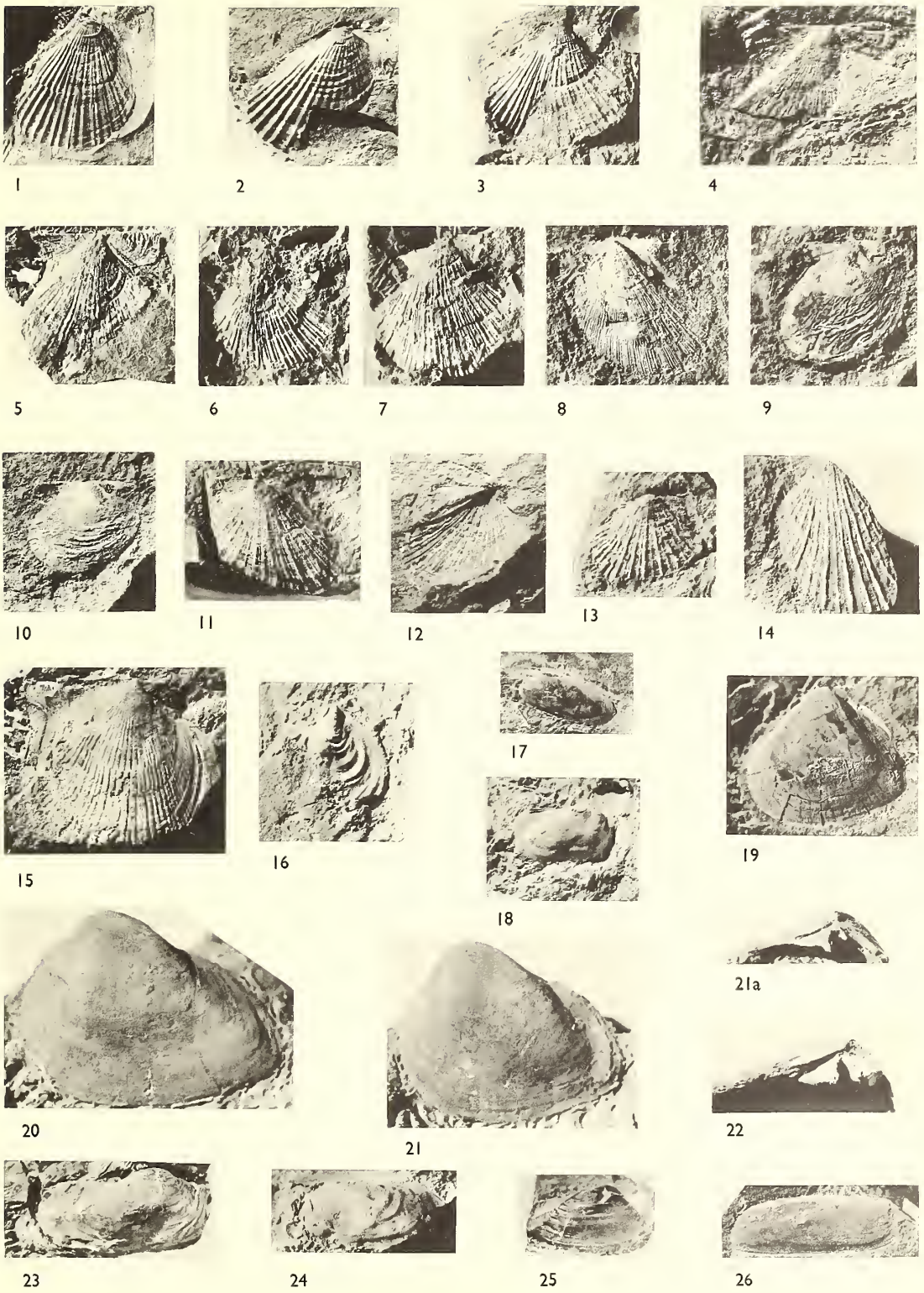
of the posterior ear markedly falcate. The anterior ear is not so well preserved as depicted by Hind. This specimen was referred to the American species *Aviculopecten whitei* Meek which is now the type species of *Dunbarella* (Newell 1938, p. 38). Good illustrations of *Dunbarella whitei* were given by Newell (op. cit., pl. 2, figs. 12–18) showing a general resemblance to the Scottish form but differing radically in the outline of the posterior ear. Also the ears of *D. whitei* lack costae, whereas the posterior ear of the Scottish specimen possesses numerous fine costae. The shape of the Scottish specimen's posterior ear is not typical of the genus *Dunbarella* and the form is best referred to for the present as *Dunbarella*?

Posidoniella laevis (Brown), pl. 1, fig. 15. Hind's illustration of the specimen GSE 6437, from the foregoing locality, is misleading. It portrays what is probably a left valve, showing the upper part of the anterior margin present. This gives the impression that the umbo is terminal, thus justifying his placing this specimen in the genus *Posidoniella*. The shell (Plate 66, fig. 16) does in fact possess a small anterior ear but the remainder

EXPLANATION OF PLATE 66

All illustrations are unretouched photographs. The specimens are in the Geological Survey Collection, Edinburgh.

- Figs. 1, 2. *Palaeolima* cf. *simplex* (Phillips). 1, From Pit Shaft, Fireclay Works, Castlecary, GSE 6436, $\times 1.5$. 2, From No. 1 Marine Band, Passage Group, Gartarry Borehole, Clackmannanshire, GSE 11488, $\times 2$.
- Figs. 3–7. *Aviculopecten regularis* Hind, all from Polton Marine Band, Bilston Burn, Midlothian. 3, GSE 6419, lectotype, left valve, $\times 1.5$. 4, GSE 6420, syntype, right valve, $\times 2$. 5, GSE 11641, right valve, $\times 1.5$. 6, GSE 11639, left valve, $\times 1.5$. 7, GSE 11610, left valve, $\times 1.5$.
- Figs. 8–10. *Euchondria bilstonensis* sp. nov., same locality. 8, GSE 11611, holotype, left valve, $\times 2$. 9, GSE 11605, paratype, right valve, $\times 2$. 10, GSE 11617, right valve, $\times 2$.
- Figs. 11–14. *Pterinopectinella obliqua* Hind, same locality. 11, GSE 6418, lectotype, left valve, $\times 1.5$. 12, GSE 6417, counterpart of previous specimen, internal view of left valve, $\times 1.5$. 13, GSE 11891, right valve, $\times 1.5$. 14, GSE 11892, part of left valve showing spines on antero-ventral margin, $\times 1.5$.
- Fig. 15. *Dunbarella*? , Passage Group, River Avon, 2 miles north of Linlithgow, GSE 6452, right valve, $\times 1.5$.
- Fig. 16. *Posidonia corrugata*? (Etheridge jun.), same locality, GSE 6437, probably a left valve, $\times 2.5$.
- Fig. 17. *Promytilus*? cf. *emaciatius* (de Koninck), Passage Group, Torwood Glen, Stirlingshire, GSE 6430, left valve, $\times 2$.
- Fig. 18. *Parallelodon semicostatus* (M'Coy), Passage Group, River Avon, 2 miles north of Linlithgow, GSE 6427, right valve, $\times 1.5$.
- Fig. 19. *Schizodus* aff. *obliquus* (M'Coy), Passage Group, Greenfoot Quarry, Glenboig, Lanarkshire, GSE 6447, left valve, $\times 1.5$.
- Figs. 20–22. *Schizodus taiti* sp. nov. 20, No. 2 Marine Band, Passage Group, Kincardine Bridge Borehole, Stirlingshire, GSE 11334, holotype, left valve, $\times 1.5$. 21, Same locality and horizon, GSE 11335, paratype, left valve, $\times 1.5$. 21a, Same specimen, showing dentition, $\times 2$. 22, No. 2 Marine Band, Passage Group, Mossneuk Borehole, Stirlingshire, GSE 2666, hinge of left valve showing dentition, specimen fluoritized in hydrofluoric acid, $\times 2$.
- Fig. 23. *Sanguinolites* aff. *abdenensis* Etheridge jun., Passage Group, Torwood Glen, Stirlingshire, GSE 6455, right valve, $\times 1$.
- Fig. 24. *Sanguinolites tricostratus*? (Portlock), Passage Group, River Avon, 2 miles north of Linlithgow, GSE 6456, left valve, poorly preserved, $\times 1$.
- Fig. 25. *Sanguinolites argutus*? (Phillips), Gain Quarry, Glenboig, Lanarkshire, GSE 6474, right valve, $\times 2$.
- Fig. 26. *Prothyris* sp. nov., same locality, GSE 6442, right valve, $\times 1.5$.



WILSON, Scottish Namurian (E₂) lamellibranchs

of the anterior and ventral margins are absent. It is here determined as *Posidonia corrugata*? (Etheridge jun.).

Myalina verneuili (M'Coy), pl. 1, fig. 16. The figured specimen, GSE 6433, is from a horizon 9 to 10 feet above the Castlecary Limestone in Torwood Glen, Stirlingshire. It is a large, badly crushed, incomplete specimen of *Myalina* but it is specifically indeterminate.

Nuculana laevistriata (Meek and Worthen), pl. 1, fig. 17. The figured specimen, GSE 6433, is from a bed of shale in the River Avon, between the outcrop of the Castlecary Limestone and the railway viaduct, 2 miles north of Linlithgow. It is poorly preserved but can be doubtfully referred to the form commonly occurring in the Upper Limestone Group and known as '*Nuculana*' *levistriata*. It could also be referred to *Nuculana intermedia* Etheridge jun., but in a recent study of the Scottish lamellibranch species erected by Etheridge jun. (Wilson, in press), no type material of this species could be found, so that it is not an entirely satisfactory name. Meek and Worthen's species, *levistriata*, is from the Lower Carboniferous of North America and even if the similar form in the Scottish Upper Limestone Group proves to be conspecific with it, its presence in the Passage Group is not really important to the main discussion.

Nucula gibbosa Fleming, pl. 1, figs. 18, 19. The figured specimen, GSE 6434, from Gain Quarry, Glenboig, Lanarkshire, is a poorly preserved internal mould of *Nuculopsis gibbosa* (Fleming). This species occurs through much of the Lower Carboniferous of Scotland and need not be further considered.

Modiola subelliptica (Meek), pl. 1, fig. 20. The specimen illustrated, GSE 6430, from a horizon 9 to 10 feet above the Castlecary Limestone, Torwood Glen, is refigured (Plate 66, fig. 17). Hind referred it to Meek's American species *subelliptica* which Newell (1942, pp. 42, 43) designated as the type species of *Volsellina* Newell. The Scottish specimen is unlike *V. subelliptica*, lacking the angular umbonal ridge, and its hinge line is relatively much shorter. It is a slightly crushed left valve, approximately 7.5 mm. long and 3.7 mm. high. The umbo is terminal or subterminal, raised slightly above the hinge-line and is crushed. British Carboniferous Modiolids are in need of revision, and for the present this form is doubtfully referred to *Prouytilus*? *emacius* (de Koninck).

Parallelodon [*Grammatodon*] *tenuistriata* (Meek and Worthen), pl. 1, fig. 21. The figured specimen, GSE 6427, is from the right bank of the River Avon, between the outcrop of the Castlecary Limestone and the railway viaduct. It is a poorly preserved internal mould (Plate 66, fig. 18), with two postero-lateral teeth present, but the outline is incomplete in places and the anterior end is crushed. It is clear, however, that it is not so relatively elongate as the American species *tenuistriata*. It is here referred to *Parallelodon seuicostatus* (M'Coy) on the evidence of the general valve shape. This latter species is of common occurrence at some horizons in the Scottish Upper Limestone Group. Hind also claimed to have recognized the American species in the Polton Marine Band at Bilston Burn, but this record has already been changed to *P. seuicostatus* (Wilson in Tulloch and Walton 1958, p. 89).

Protoschizodus curtus (Meek and Worthen), pl. 1, figs. 22, 23. Of the specimens figured, GSE 4506, represented by fig. 23, is crushed, incomplete, and can only be identified as *Schizodus* sp. The other specimen, GSE 6447, illustrated as fig. 22, preserved in ironstone and uncrushed, is from Greenfoot Quarry near Gain Farm, Glenboig,

Lanarkshire. It is refigured (Plate 66, fig. 19) and is different in valve outline from *Schizodus curtus* as shown by Meek (*in* Hayden 1872, pl. 10, fig. 13), particularly at the anterior end. The Scottish specimen has a straight upper antero-dorsal margin whereas the American species appears to have a symmetrically curved anterior border and an anterior umbonal ridge. The Scottish form is here determined as *Schizodus* aff. *obliquus* (M'Coy) but it probably represents an undescribed species.

Schizodus wheeleri (Swallow), pl. 1, figs. 24–28. Of the specimens figured by Hind, GSE 8517 (fig. 24) is incomplete at the posterior end, GSE 8518 (fig. 25) has decayed in storage, GSE 6458 (fig. 26) is poorly preserved and only shows the hinge, GSE 6457 (fig. 27) is crushed and incomplete, and GSE 6459 (fig. 28) has the posterior end and umbo missing. These specimens were presumably in better condition when Hind examined them. The form he described and illustrated is easily recognized in modern collections from the marine bands near the base of the Passage Group in Stirlingshire and Clackmannanshire. The present writer regards this form as different from other described British species of *Schizodus* and different from the American species *S. wheeleri*. It is described below as *Schizodus taiti* sp. nov.

? *Anthraconyia truncata* Hind, pl. 1, figs. 29, 30. The specimens GSE 11381, 2, represented by figs. 29 and 30 respectively, are poor but are here determined as *Curvirimula* aff. *belgica* (Hind). They are in a dark shale from a drain in the bottom of Greenfoot Quarry near Gain Farm, Glenboig, and the horizon is probably near the top of the Upper Limestone Group. *C. belgica* has been figured by Weir (1960, pl. 32, fig. 47) from about this horizon.

Edmondia excentrica Hind, pl. 2, figs. 31, 32. Of the figured specimens, GSE 6422 (fig. 31) is poorly preserved and the margins are incomplete and GSE 6421 (fig. 32) is a young shell with the postero-dorsal margin missing so that the outline shown by Hind is not a true one. Both specimens are here identified as *Edmondia unioniformis*? (Phillips).

Edmondia sulcata (Phillips), pl. 2, fig. 33. The figured specimen, GSE 6426, is a poorly preserved internal mould and the margin is incomplete except at the posterior end. It is here identified as *Wilkingia elliptica*? (Phillips). Hind did not claim American affinities for these last three species.

Edmondia uebrascensis (Geinitz), pl. 2, fig. 34. The figured specimen, GSE 6424, is from No. 3 Marine Band, Passage Group, in the Rosehill Diamond Bore, Plean, Stirlingshire. It is preserved in shale and is crushed and incomplete, but it is here identified as *Edmondia* cf. *maccoyi* Hind. Hind (1908, p. 358) stated that *E. maccoyi* is closely related to the American species *E. uebrascensis* and that the Scottish specimens he had available were poorly preserved. He said that the former was more gibbose and that the ornament was different. The specimens he examined are all crushed and the true gibbosity cannot be seen; also their preservation is such that the shell markings are too poor to justify reference to an American species. Subsequent collections from the same strata in the area have yielded specimens which have been determined as *E. cf. maccoyi* (Wilson *in* Read 1959, pp. 67, 68).

Edmondia lyelli Hind, pl. 2, fig. 35. The figured specimen, GSE 6423, is crushed and incomplete but Hind's determination is confirmed. No American affinities were claimed for this species.

Sanguinolites occidentalis Meek and Hayden, pl. 2, figs. 36–38. Hind used three

specimens from different localities to illustrate this form. GSE 6455 is from a horizon 9 to 10 feet above the Castlecary Limestone in Torwood Glen, Stirlingshire. It is crushed and incomplete with a well-defined umbonal ridge, and the postero-dorsal region is concave. It probably represents an undescribed species but has affinities with *Sanguinolites abdenensis* Etheridge jun. (Plate 66, fig. 23). GSE 7563 (fig. 37) is incomplete and so poorly preserved as to be indeterminate. GSE 6456 (fig. 38) is an internal mould preserved in a weathered ironstone from above the Castlecary Limestone from the right bank of the River Avon between the outcrop of that Limestone and the railway viaduct, near Linlithgow. It is poorly preserved but is here determined as *Sanguinolites tricosatus*? (Portlock) (Plate 66, fig. 24). The illustration by Meek (*in* Hayden 1872, pl. 10, fig. 12) of *Pleurophorus occidentalis* shows a valve with a prosogyrous umbo placed almost at the anterior end and the shell expands rapidly in height towards the posterior. None of the Scottish specimens has these characters.

?*Allorisma reflexa* Meek, pl. 2, fig. 39. The figured specimen, GSE 6410, is a fragment of an internal mould of a right valve of a lamellibranch with concentric markings. The only part of the margin of the shell present is a small length of the venter. The specimen is extremely poorly preserved but is most likely to be a part of *Sanguinolites* cf. *clavatus* (Etheridge jun.).

Tellinomorpha hindii Bolton, pl. 2, figs. 40–42. Hind illustrated three specimens of this form, all preserved as internal moulds in ironstone, from Gain Quarry, 1 mile NNE. of Glenboig, Lanarkshire. GSE 6475 (fig. 40) is an almost complete right valve. GSE 6476 (fig. 41) is a left valve with the posterior end missing, although Hind portrayed it as complete. GSE 6474 (fig. 42) is a right valve and the venter has now been cleared of matrix. Hind did not claim American affinities for this form but compared it with a species described from a marine band near the base of the Coal Measures of Bristol by Bolton (1907, p. 460, pl. 30, fig. 8a, b). The Scottish specimens, however, have a tapering posterior end and a relatively longer anterior end than Bolton's species and the writer regards them as distinct. Hind (1900, p. 431) distinguished *Tellinomorpha* from *Sanguinolites* by the absence of an oblique ridge in the former, but the valves under discussion have a distinct umbonal ridge (Plate 66, fig. 25). Hind (1908, p. 350) claimed to have seen tubercles on these Scottish specimens but these are not visible now. The specimens bear a close resemblance to *Sanguinolites argutus* (Phillips) but are only doubtfully referred to that species which itself is based on poor material.

Solenomorpha cylindrica Hind, pl. 2, figs. 43, 44. Hind (1908, pp. 350–1) described this species from two specimens from Greenfoot Quarry, Gain Farm, Glenboig. The syntypes, GSE 6445 and 6460, are extremely poor internal moulds preserved in ironstone and it is thought that Hind's drawings are restorations based on insufficient evidence. These specimens are here determined as *Solenomorpha* sp.

Solenomya brevis Hind, pl. 2, figs. 45–47. This species was described from three specimens, GSE 6461–3, all poorly preserved internal moulds in ironstone, from the foregoing locality. Two are young individuals and the third is incomplete; GSE 6463 (fig. 45) is the only valve with the outline complete. The only character which differentiates these specimens from *Solenomya excisa* de Koninck, as figured by Hind (1900, pl. 50, figs. 11, 12, 14–16), is the lack of radial striae. It is possible that such striae would not be seen on poorly preserved internal moulds, and the specimens are here identified as *S. excisa*?

Prothyris elegans Meek, pl. 2, figs. 48–50. Hind used three specimens to illustrate this form, GSE 6442–4. All are internal moulds preserved in ironstone from the same locality as before. The best specimen, GSE 6442 (fig. 50), is refigured (Plate 66, fig. 26). Hind (1908, p. 353) claimed that these Scottish specimens of *Prothyris* were conspecific with the American species *P. elegans* and laid great stress on this occurrence when he concluded that a fauna with strong American affinities was present in the Passage Group. *P. elegans* is stated by Meek (*in* Hayden 1872, p. 223) to have the length about three times the height. The Scottish specimens have the length slightly less than three times the height. This ratio is similar to that in *P. soleniformis* Elias, but judging by the illustration of the holotype of that species (Elias 1957, pl. 90, fig. 3), the Scottish form differs in valve outline, especially at the posterior end. The present writer thinks that these Scottish specimens belong to an undescribed species, and as he is engaged at present in reviewing the occurrence of *Prothyris* in Britain, the form under discussion is here referred to as *Prothyris* sp. nov.

Solenomya cylindrica Hind, pl. 2, figs. 60, 61. Two specimens, GSE 6464–5, were figured and both are internal moulds in ironstone from the same locality. Hind (1908, pp. 351–2) described the species on the evidence of these two specimens, pointing out that it was closely related to *Solenomya costellata* (M'Coy). The writer claims that the specimens are too poorly preserved to be distinguished from the latter species and they are here doubtfully referred to it.

Gastropods. Loxonema nanum de Koninck, pl. 2, fig. 51. The figured specimen GSE 6263 is the internal mould of a small, high-spined gastropod, but only two whorls remain. It is now indeterminate, and as it is an internal mould, it probably was also indeterminate when Hind examined it.

Naticopsis brevispira de Ryckholt, pl. 2, figs. 52, 53. The figured specimens, GSE 6279 and 6285, are small, incomplete, and poorly preserved and are here determined as *Naticopsis*?

Ptychomphalus marcouianus (Geinitz), pl. 2, fig. 55. The specimen figured, GSE 6286, was referred to the Scottish species *Glabrocingulum armstrongi* Thomas by Thomas (1940, p. 42).

Bellerophon marcouianus Geinitz, pl. 2, fig. 56. The figured specimen, GSE 6266, was redescribed as *Bellerophon torwoodensis* Weir by Weir (1931, p. 812), who rejected Hind's claim that the specimen belonged to the American species of Geinitz.

Euphemus d'orbignyi (Portlock), pl. 2, figs. 57, 58. The figured specimen, GSE 6265, was cited by Weir (1931, p. 849) as *Euphemus urei* (Fleming) mut. *hindi* Weir. This name was changed by Wilson (*in* Read 1959, p. 64) to *Euphemites hindi* (Weir).

Macrocheilina sp., pl. 2, fig. 59. The figured specimen is missing but as Hind did not claim American affinities for it, it can be ignored.

Scaphopod. Entalis meekianum (Geinitz), pl. 2, fig. 54. The figured specimen, GSE 6795, is 23 mm. long, slightly curved, but both ends are broken. The exposed surface is smooth but the removal of some matrix revealed faint oblique striae, suggesting that the specimen may be determined as *Dentalium (Plagioglypta)* sp., but it is too poor to be compared with American species.

The revised names of the specimens figured by Hind are listed below together with Hind's names.

HIND'S NAME AND FIGURE NO.	REVISED NAME
1. <i>Palaeolima retifera</i> (Shumard)	<i>Palaeolima</i> cf. <i>simplex</i> (Phillips)
2, 3. <i>Aviculopecten regularis</i> Hind	<i>Aviculopecten regularis</i> Hind
4-7. ? <i>Aviculopecten neglectus</i> (Geinitz)	<i>Euchondria bilstonensis</i> sp. nov.
8. <i>Aviculopecten obliquus</i> Hind	<i>Pterinopectinella obliqua</i> (Hind)
9, 10. <i>Limatulina alternata</i> (M'Coy)	' <i>Limatulina</i> ' <i>alternata</i> (M'Coy)
11-13. <i>Pterinopecten whitei</i> (Meek)	<i>Dunbarella</i> ?
15. <i>Posidoniella laevis</i> (Brown)	<i>Posidonia corrugata</i> ? (Etheridge jun.)
16. <i>Myalina verneuili</i> (M'Coy)	<i>Myalina</i> sp.
17. <i>Nuculana laevistriata</i> (Meek and Worthen)	? <i>Nuculana intermedia</i> (Etheridge jun.)
18, 19. <i>Nucula gibbosa</i> Fleming	<i>Nuculopsis gibbosa</i> (Fleming)
20. <i>Modiola subelliptica</i> (Meek)	<i>Promytilus</i> ? cf. <i>emaciatum</i> (de Koninck)
21. <i>Grammatodon tenuistriata</i> (Meek and Worthen)	<i>Parallelodon semicostatus</i> (M'Coy)
22, 23. <i>Protoschizodus curtus</i> (Meek and Worthen)	<i>Schizodus</i> aff. <i>obliquus</i> (M'Coy)
24-28. <i>Schizodus wheeleri</i> (Swallow)	<i>Schizodus taiti</i> sp. nov.
29-30. ? <i>Anthracomya truncata</i> Hind	<i>Curvirimula</i> aff. <i>belgica</i> (Hind)
31, 32. <i>Edmondia excentrica</i> Hind	<i>Edmondia unioniformis</i> ? (Phillips)
33. <i>Edmondia sulcata</i> (Phillips)	<i>Wilkingia elliptica</i> ? (Phillips)
34. <i>Edmondia nebrascensis</i> (Geinitz)	<i>Edmondia</i> cf. <i>maccoyi</i> Hind
35. <i>Edmondia lyelli</i> Hind	<i>Edmondia lyelli</i> Hind
36. <i>Sanguinolites occidentalis</i> (Meek and Hayden)	<i>Sanguinolites</i> aff. <i>abdenensis</i> Etheridge jun.
38. <i>Sanguinolites occidentalis</i> (Meek and Hayden)	<i>Sanguinolites tricostatus</i> ? (Portlock)
39. ? <i>Allorisma reflexa</i> Meek	<i>Sanguinolites</i> cf. <i>clavatus</i> (Etheridge jun.)
40-42. <i>Tellinomorpha hindii</i> Bolton	<i>Sanguinolites argutus</i> ? (Phillips)
43, 44. <i>Solenomorpha cylindrica</i> Hind	<i>Solenomorpha</i> sp.
45-47. <i>Solenomya brevis</i> Hind	<i>Solemya excisa</i> de Koninck
48-50. <i>Prothyris elegans</i> Meek	<i>Prothyris</i> sp. nov.
50, 51. <i>Solenomya cylindrica</i> Hind	<i>Solemya costellata</i> ? (M'Coy)
51. <i>Loxonema nanum</i> de Koninck	Indeterminate
52, 53. <i>Naticopsis brevispira</i> de Ryckholt	<i>Naticopsis</i> ?
54. <i>Entalis meekianum</i> (Geinitz)	<i>Dentalium (Plagioglypta?)</i> sp.
55. <i>Ptychomphalus marcouianus</i> (Geinitz)	<i>Glabrocingulum armstrongi</i> Thomas
56. <i>Bellerophon marcouianus</i> Geinitz	<i>Bellerophon torwoodensis</i> Weir
57, 58. <i>Euphemus d'orbignyi</i> (Portlock)	<i>Euphemites hindi</i> (Weir)
59. <i>Macrocheilina</i> sp.	missing

SYSTEMATIC PALAEONTOLOGY

Genus EUCHONDRIA Meek 1874

Euchondria bilstonensis sp. nov.

Plate 66, figs. 8-10

?Aviculopecten neglectus Hind 1908, pp. 341-2, pl. 1, figs. 4-7.*Euchondria* sp. nov. Wilson in Tulloch and Walton 1958, p. 89.

Material. Holotype: GSE 11611, a left valve. Paratype: GSE 11605, a right valve.

Locality. The species is only known from one locality, the Polton Marine Band, on the right bank of the Bilston Burn, 220 yards S. 30° W. of south-west corner of Bilston Lodge, Polton, near Edinburgh. The horizon is 27 to 30 feet above the Castlecary Limestone, of Namurian (E₂) age, Upper Carboniferous. There are numerous examples of the species in the Geological Survey Collection, Edinburgh, but none is well preserved.

Description. Left valve: moderately convex, maximum convexity is in sub-umbonal region, markedly prosocline. Length is approximately equal to height. Hinge-line straight, 7 mm. long in a valve approximately 11 mm. long. Umbonal folds are moderately well developed and there is an outward angular fold on the posterior ear, running from the umbo to half-way down the posterior margin of the ear. Ears are equal in length, anterior one triangular with fine costae, posterior one also has fine costae and its posterior margin forms an obtuse angle about the termination of the angular fold. Body of valve has numerous, regularly spaced, fine, intercalate costae with irregularly spaced fine fila present, seen in the ventral region of the holotype. Preservation is not good but some specimens appear to show small pits on the ligament area, a characteristic feature of *Euchondria*. Umbonal angle is approximately 90 degrees.

Right valve: almost as convex as left valve, with maximum convexity in sub-umbonal area. The outline is the mirror image of the left valve except for the byssal sinus under the anterior ear. The inner margin of the posterior ear is marked by a straight, sharp, indented fold corresponding to the outward fold in the left valve. An angular ridge runs from the umbo to half-way down the posterior margin. Anterior umbonal fold is moderately well developed. Valve marked by obscure growth-lines only. Anterior ear bears irregularly spaced costae, maximum number seen is five, crossed by close-spaced fila. Posterior ear appears to have fine costae only. Poorly preserved small ligament pits are present on some of the specimens.

Discussion. Hind (1908, p. 342), with only a few poorly preserved specimens available, deduced that the costate left valves and almost smooth right valves of the form just described belonged to the same species. The writer, having examined numerous specimens of the Pectinid shells from the locality, confirms this view. Although no attached valves have yet been seen, there are cases where left and right valves are very closely associated. Hind referred the form to *Pecten neglectus* Geinitz, a Pennsylvanian species from Nebraska which is now the type species of the genus *Euchondria* Meek and was redescribed by Newell (1938, pp. 104-5). Hind also suggested that the costate left valve figured by Meek (*in* Hayden 1872, pl. 9, fig. 2a) as *Aviculopecten coxanus* (Meek and Worthen) was the left valve of *A. neglectus*, an opinion also expressed by Newell (1938, p. 104). The costae of the left valve of *E. bilstonensis* are much more closely spaced and the valves are much more prosocline than in *E. neglectus*. Although of common occurrence at the type locality, *E. bilstonensis* has not yet been recorded elsewhere.

Genus SCHIZODUS de Verneuil 1844

Schizodus taiti sp. nov.

Plate 66, figs. 20–22

Schizodus wheeleri, Hind 1908, pp. 345–6, pl. 1, figs. 24–28.

Material. Holotype: GSE 11334, a left valve. Paratype: GSE 11335, a left valve. Both specimens from No. 2 Marine Band, Passage Group, Upper Carboniferous, in Kincardine Bridge Borehole, Stirling-shire.

Description. A medium-sized species of *Schizodus*, elongate, inequilateral, subtrigonal, posterior end produced. Umbones situated in anterior quarter, small, incurved, slightly prosogyrous. Sub-umbonal region convex, remainder only slightly convex except for a pronounced subangular umbonal ridge, running to postero-ventral extremity. Anterior and posterior cardinal margins make an obtuse angle of about 125 degrees about the umbo. Anterior border is symmetrically curved, ventral margin gently convex and meets the almost straight, truncate posterior margin in an acute angle of about 60 degrees. The dentition has only been seen in the left valve in which it consists of a large central tooth, which is bifid when traced under the umbo, and a small one to the anterior. Their notation in the system used by Cox (1951, p. 363) is 2, 4a, and the cavity which separates them presumably accommodated the large central tooth 3a of the right valve. In the left valve a slight thickening of the postero-cardinal margin may be a poor expression of tooth 4b. Shell about 1 mm. thick in large specimens. Exterior marked by fine growth-lines only. Interior has not been seen. Dimensions of holotype—length 28 mm., height 21 mm., width (of one valve) 8 mm.

Discussion. *Schizodus taiti* has a distinctive shape and can be distinguished from other British described species by its produced posterior end and the long, almost straight, ventral margin. Hind (1908, p. 346) referred the Scottish specimens to *S. wheeleri* (Swallow) as depicted by Meek (*in* Hayden 1872, pl. 10, figs. 1a–f) claiming that the range of variation shown by the American forms could be matched by the Scottish material. An examination of the specimens used by Hind has shown that none is complete and many are crushed so that he had not adequate material to make this claim. Only the specimen GSE 8517 (Hind 1908, pl. 1, fig. 24) is good enough to show the general shape of the valve and it is incomplete posteriorly. The illustrations of *S. wheeleri* by Meek (*op. cit.*) show a great range of variation in shape suggesting that more than one species is involved. Judging by the plate explanation, only fig. 1b, a drawing of a specimen in the possession of Swallow, can be taken to depict the characters of *S. wheeleri*. This shows a left valve with the ventral margin markedly upturned posteriorly, a relatively large postero-dorsal area and a poorly inflated subumbonal region, features absent in the Scottish specimens. Indeed the shape of *S. taiti* is quite different from all the variable shapes ascribed to *S. wheeleri* by Meek.

Elias (1958, p. 26) referred the Scottish specimens to *S. cf. batesvillensis* Weller but this latter species is much more elongate than *S. taiti*. *S. taiti* is of common occurrence in Namurian (E₂) beds of the Scottish Central Coalfield, ranging from the Calmy Limestone, in the Upper Limestone Group, up to No. 3 Marine Band in the Passage Group.

CONCLUSIONS

The re-examination of the specimens which Hind figured to illustrate the Scottish fauna which he claimed had strong North American Upper Carboniferous affinities, has shown two things. The first is that many of the specimens are poorly preserved and, in the writer's opinion, are not good enough to base such far-reaching conclusions upon. Secondly, the specimens which can be identified specifically are now referred to species which were first described from British material, many from the Lower Carboniferous. What Hind (1908, p. 332) said regarding the lamellibranch fauna was: 'Quite 50 per cent. of the species were, as far as I could discover, new to Europe, but which resembled very closely the lamellibranch fauna of the Coal Measures of Nebraska and Illinois of North America. The most striking member of the fauna was the shell *Prothyris elegans* Meek, this being the first occurrence of the genus in the Carboniferous rocks of Great Britain.' It must be remembered that Hind was confronted with these specimens from the Passage Group just after he had finished his monograph of the British Carboniferous Lamellibranchiata. The presence of *Prothyris*, a genus he had not met with in the preparation of his monograph, turned his attention to American works, particularly to that of Meek (*in* Hayden 1872) on the Upper Carboniferous fossils of Nebraska, a profusely illustrated work. The writer thinks that Hind, having convinced himself that he had one member of Meek's Nebraskan fauna, hitherto unrecorded from Britain, referred a few poorly preserved specimens of other genera to American species.

It is unfortunate that so much stress was laid on the presence of *Prothyris*. This genus is now known to occur in the Midland Valley in the Limestone Coal Group, Namurian E₁ (Pringle *in* Allan and Knox 1934, p. 121), and in Dumfriesshire two species have been recognized about 2,000 feet below the base of the Upper Carboniferous (Wilson 1961, *in press*).

The writer claims that Hind was mistaken in his reference of approximately half the molluscan species found in the marine bands in the lower part of the Passage Group to American forms. The conclusion now drawn is that in the upper part of the Arnsbergian (E₂) Stage of the British Namurian, while the goniatite and thin-shelled lamellibranch faunas flourished in the Pennine area, a rich fauna of molluscs and calcareous brachiopods lived in the Scottish Midland Valley area. Also, the composition of this fauna suggests that it is a continuation of the type of faunas found in earlier Scottish Carboniferous strata, since many of the species and all of the genera are present in Scottish Lower Carboniferous rocks. Thus there is no need to invoke a migration of species from North America to Scotland in Lower Carboniferous times as suggested by Elias (1958, p. 27). Elias (*op. cit.*, p. 26) revised Hind's identifications of the figured specimens, and although he changed some of the American names to British ones, he referred some forms to American species described after Hind's paper was published. Unfortunately, Elias was under the impression that the figured specimens were well preserved and the illustrations were accurate. For example, these assumptions led Elias to refer the four illustrations by Hind (1908, pl. 1, figs. 4-7) of the species now named *Euchondria bilstonensis* sp. nov., to three species of *Aviculopecten* and one of *Deltopecten*?. The revised identifications suggested by Elias have not been ignored, but the present list of revised determinations is based on a study of the actual specimens used by Hind together with numerous other specimens from the same localities and horizons.

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SOME FORAMINIFERA FROM THE AMPTHILL CLAY, UPPER JURASSIC, OF CAMBRIDGESHIRE

by W. A. GORDON

ABSTRACT. Seventeen species of foraminifera are recorded from two samples of Ampthill Clay collected at Knapwell and Mepal, Cambridgeshire. One species is new. The foraminifera are compared with those of the sandy-calcareous facies of the Corallian Beds seen on the Dorset coast.

THE present paper is the first published work on the foraminifera of the Ampthill Clay, Oxfordian, Upper Jurassic, of England. It arises from a broader study of the Corallian foraminifera of southern England which was made for a Ph.D. thesis in the University of London.

Previous work on foraminifera from the Oxfordian rocks of England includes two useful papers by Barnard (1952, 1953) on the Upper Oxford Clay of Warboys, Huntingdonshire, and Redcliff Point, Dorset. Less valuable are the faunal lists published without illustration by Jones and Parker (1875), Whitaker (1886), and Crick (1887). The only other work is that by Sherborn (1888) on an adherent foraminifer from the Oxford Clay near Weymouth.

The material which forms the basis of the present paper was collected from the Ampthill Clay at the only two places where it could be found exposed at the surface, at Knapwell and at Mepal, both in Cambridgeshire. The exposure at Knapwell has been discussed by Hancock (1954) who recorded an ammonite fauna comprised of *Decipia lintonensis*, *D. decipiens*, and *Pseudarisphinctes spp.* He considered that the fauna represents a horizon above the Boxworth Rock and that it correlates with the upper part of the *Trigonia clavellata* beds of Dorset. The position of the Mepal exposure within the local Ampthill sequence is not known, but it is presumably equivalent to part of the Glos Oolite Series of Dorset. Details of the rock samples which were studied for their foraminifera are as follows:

- (a) Knapwell Stream, Knapwell, Cambs. (Grid Ref. 52/331641). Dark-grey clay containing many selenite crystals. Fairly shelly. Stratigraphical thickness sampled: 24 inches.
- (b) Toll Farm, Mepal, Cambs. (Grid Ref. 52/435813). Shelly dark grey clay. Stratigraphical thickness sampled: 8 inches.

Two hundred and twenty-three foraminifera were obtained from the Knapwell sample, and 307 from the Mepal sample. In addition to the foraminifera, both samples yielded ostracods abundantly, and the Mepal material included a number of crinoid ossicles, holothurian spicules, and a segment of the whorl of a small ammonite. In both samples there were many fragments of oyster and other lamellibranch shells.

Figured specimens of the foraminifera will be presented to the British Museum (Natural History).

SYSTEMATIC DESCRIPTIONS

Family LITUOLIDAE

Genus CRIBROSTOMOIDES Cushman 1910

Cribrostomoides canui (Cushman)

Text-fig. 1 (1)

1929 *Haploplragmoides canui* Cushman, p. 133, pl. 4, figs. 1a, b.1949 *Haploplragmoides canui* Cushman; Cushman and Glazevski, p. 4, pl. 1, fig. 3.1959 *Ammobaculites laevigatus* Lozo; Lloyd, p. 313, pl. 54, fig. 14; text-fig. 4a.

Material. Three damaged specimens from Mepal.

Description. The test is planispiral, umbilicate, involute, tending to become evolute in the last half whorl. The thickness of the test is about half the greatest diameter, and the test wall is fairly smoothly constructed. There are nine or ten chambers in the final whorl. The aperture appears to be elliptical, centrally placed on the apertural face.

Dimensions. Greatest diameter of the specimens, 0.56, 0.57, and 0.74 mm.

Remarks. The Amphill Clay specimens are rather larger than those described by Cushman (1929) from the Oxfordian of Calvados, Normandy, but there does not seem to be any essential difference between the two forms.

Genus AMMOBACULITES Cushman 1910

Ammobaculites agglutinans (d'Orbigny)

Text-fig. 1 (4)

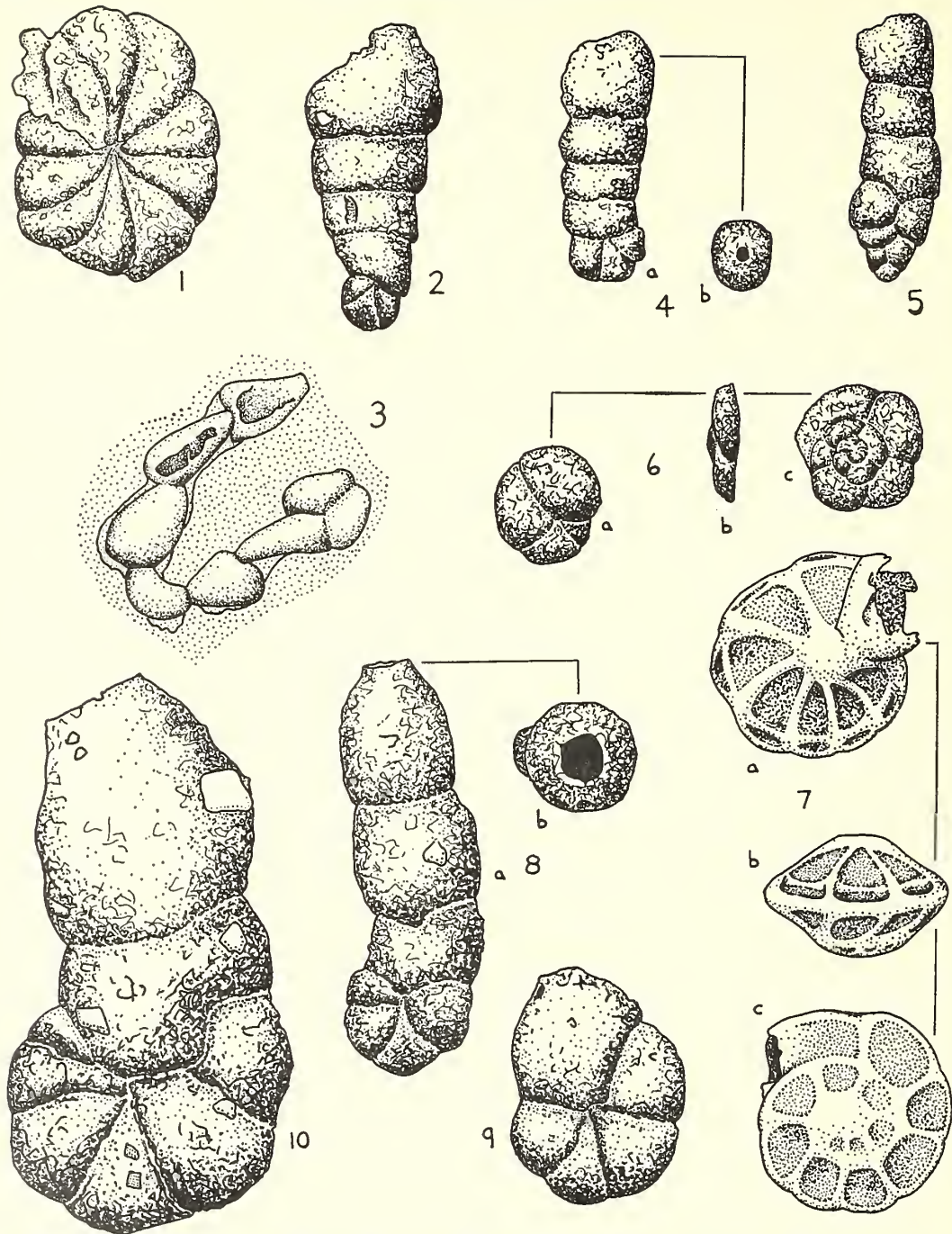
1846 *Spirolina agglutinans* d'Orbigny, p. 137, pl. 7, figs. 10–12.1932 *Ammobaculites coprolithiformis* (Schwager); Paalzow, p. 94, pl. 4, fig. 19.1937 *Ammobaculites agglutinans* (d'Orbigny); Bartenstein and Brand, p. 186, pl. 4, fig. 14; pl. 5, figs. 7, 8; pl. 6, figs. 40a, b; pl. 8, figs. 38a, c; pl. 10, figs. 45a, b; pl. 11A, figs. 19a, b; pl. 11B, figs. 28a, b; pl. 12A, fig. 22; pl. 13, fig. 23; pl. 14B, fig. 19.1943 *Ammobaculites agglutinans* (d'Orbigny); Ströbel (pars), p. 14, pl. 12, fig. 22.1959 *Ammobaculites agglutinans* (d'Orbigny); Lloyd, p. 309, pl. 54, figs. 9, 11 (? 10); text-figs. 4b, d, e (? c).

Material. Eleven specimens from Mepal.

Description. The test is slightly compressed and consists of a coil of three to five chambers followed by a rectilinear or curvilinear series of four or five chambers. The coil is usually about one-third of the size of the whole test, but it may be as much as half the test. It is angular in outline, sometimes umbilicate, and the chambers are often indistinct. The uncoiled part has depressed sutures, the chambers being irregular in form but commonly drum-shaped. The last formed chambers are often inflated. The wall of the test is roughly constructed of irregularly sized particles. The aperture is central, terminal, circular, with an internal lip of white calcite.

Dimensions. Length, 0.43–0.62 mm.

Remarks. The original description of this species was by d'Orbigny from the Tertiary of the Vienna Basin. In the Jurassic, forms which appear to be indistinguishable from the Tertiary species occur at least from the Bajocian to the Kimmeridgian.



TEXT-FIG. 1. (1) *Cribrostomoides canui* (Cushman). Mepal. $\times 60$. (2) *Annobaculites* cf. *reophiaciformis* Cushman. Mepal. $\times 60$. (3) *Bullopora rostrata* Quenstedt. Knapwell. $\times 60$. (4)a, b. *Ammobaculites agglutinans* (d'Orbigny). Mepal. $\times 75$. (5) *Bigenerina* cf. *nodosaria* d'Orbigny. Mepal. $\times 75$. (6)a-c. *Trochammina squamata* Jones and Parker. Mepal. $\times 75$. (7)a-c. *Voorthuysenia tenuicostata* (Bartenstein and Brand). Mepal. $\times 75$. (8)a, b. *Ammobaculites coprolithiformis* (Schwager). Mepal. $\times 40$. (9), (10) *Ammobaculites coprolithiformis* (Schwager). Knapwell. $\times 40$.

Ammobaculites coprolithiformis (Schwager)

Text-fig. 1 (8), (9), (10)

- 1867 *Haploplragmium coprolithiforme* Schwager, p. 654, pl. 34, fig. 3.
1879 *Haploplragmium pictonicum* Berthelin, p. 26, pl. 1, figs. 1, 2.
1884 *Haploplragmium coprolithiforme* Schwager; Deecke, p. 20, pl. 1, fig. 5.
1885 *Haploplragmium coprolithiforme* Schwager; Haeusler, p. 13.
?1886 *Haploplragmium vetustum* Terquem and Berthelin; Deecke, p. 15, pl. 2, figs. 1-1e.
1886 *Haploplragmium coprolithiforme* Schwager; Deecke, p. 15, pl. 2, figs. 2-2d.
1890 *Haploplragmium coprolithiforme* Schwager; Haeusler, p. 33, pl. 4, figs. 7, 20.
1936 *Haploplragmium coprolithiforme* Schwager; Kuhn, p. 446, text-figs. 3, 4.
1939 *Ammobaculites subaequalis* Myatliuk, pp. 44, 70, pl. 2, figs. 19, 20.
1952 *Ammobaculites* cf. *coprolithiformis* (Schwager); Usbeck, p. 382, pl. 14, fig. 16.
1953 *Ammobaculites suprajurassicum* (Schwager); Barnard, p. 184, fig. A, 2a, b.
1954 *Ammobaculites coprolithiformis* (Schwager); Bielecka and Pozaryski, pp. 27, 161, pl. 3, figs. 6a, b.
1955 *Ammobaculites alaskensis* Tappan (pars), p. 43, pl. 12, figs. 1, 2, 4, 5, 9, 10.
1959 *Ammobaculites* cf. *coprolithiformis* (Schwager); Lloyd, p. 311, pl. 54, figs. 12a, b.
1959 *Ammobaculites subaequalis* Myatliuk; Lloyd, p. 311, pl. 54, figs. 16, 17.

Material. Sixty-seven specimens from Knapwell; 29 from Mepal.

Description. The test consists of a planispiral coil of two to six chambers, followed by an uncoiled series of up to six chambers. The coil makes up about one-third of the test and most commonly consists of three chambers. The uncoiled series usually begins with a drum-shaped chamber which partly embraces the coil, and this is followed by gently inflated chambers which increase irregularly in height. The uncoiled part is gently compressed and is straight, arcuate, or S-shaped. The sutures are distinct, depressed, radial on the coil, and approximately transverse on the uncoiled part. The end chamber is inflated, conical or pyriform. The wall of the test is roughly constructed, usually of quartz particles, and bound together by a white calcareous cement. The aperture is central, terminal, polygonal.

In early growth stages, the aperture resembles that of the adult in shape, but it is developed low on the apertural face in two- and three-chambered individuals. It usually becomes terminal when a fourth chamber is added.

Dimensions. Length, up to 2.13 mm.; usually between 0.8 and 1.5 mm.

Remarks. This species was first described by Schwager from the *sowerbyi* zone (Bajocian) of Württemberg. It has been recorded many times from the Oxfordian and seems to be at its greatest abundance at this level, although there are also records from the Lias of a large *Ammobaculites* which appears to belong to the same species.

Outside western and central Europe, this species has been found in the lower Volgian of the Saratov and Kuibyshev districts, U.S.S.R. (Myatliuk, 1937), the upper Oxfordian and lower Kimmeridgian of central Poland (Bielecka and Pozaryski, 1954), and the Lias and Upper Jurassic of northern Alaska (Tappan, 1955).

Specimens which have been referred to *A. coprolithiformis* (Schwager) by Colom (1952) from the Upper Cretaceous of Navarre and Soria, Spain, and by Cushman (1946) from the Upper Cretaceous of western Canada, south-eastern U.S.A., Trinidad, and Mexico, do not appear to belong to the same species.

Ammobaculites cf. *reophaciformis* Cushman

Text-fig. 1 (2)

cf. 1910 *Ammobaculites reophaciformis* Cushman, p. 440, text-figs. 12-14.

Material. One specimen from Mepal.

Description. The test consists of a small coil followed by four chambers which are arranged rectilinearly and which increase fairly rapidly in size. The coil is rounded, consisting of three chambers. The rectilinear part is slightly compressed and the chambers are drum-shaped except for the final chamber which is globular. The sutures on the rectilinear part are depressed weakly at first, more strongly later. The wall of the test is irregularly constructed of coarse, variably sized particles, and has a calcareous cement. The aperture is not preserved on the only specimen available.

Dimensions. Length of the specimen, 0.83 mm.

Remarks. This form is similar to *Ammobaculites reophaciformis* which was described by Cushman from present-day seas off the Philippine Islands, but the Ampthill Clay specimen is smaller, and the sutures are more constricted. A new species should perhaps be erected for the Jurassic form when additional material becomes available. The present author has found three other specimens of this form in the upper part of the Corallian Beds of the Dorset coast, but these were not well preserved.

Family TEXTULARIIDAE

Genus BIGENERINA d'Orbigny 1826

Bigenerina cf. *nodosaria* d'Orbigny

Text-fig. 1 (5)

cf. 1826 *Bigenerina* (*Bigenerina*) *nodosaria* d'Orbigny, p. 261, pl. 11, figs. 9-12.1890 *Bigenerina nodosaria* d'Orbigny; Haeusler, p. 73, pl. 12, figs. 1-4.

Material. Four specimens from Mepal.

Description. The test consists of six or seven biserial chambers, followed by three to five chambers arranged uniserially. The early sutures are indistinct and the test wall is roughly constructed of irregularly sized particles. The aperture is not preserved on any specimen.

Dimensions. Lengths of the specimens, 0.47, 0.49, 0.52, and 0.53 mm.

Remarks. The Ampthill Clay specimens, which are not well preserved, appear to be morphologically indistinguishable from the type of the species from the Recent, Adriatic Sea.

Family OPHTHALMIDIIDAE

Genus BULLOPORA Quenstedt 1856

Bullopore globulata Barnardcf. 1858 *Bullopore* sp. Quenstedt, p. 554, pl. 72, fig. 35.1950a *Bullopore globulata* Barnard, p. 378, fig. 1e.

Material. One specimen from Knapwell.

Dimensions. Width of the only chamber outside the initial coil, 0.13 mm.

Remarks. A single specimen, adhering to a fragment of oyster shell, is referred to this species. Apart from its smaller size, this specimen seems to be indistinguishable from the type which was described by Barnard from the Lower Lias of Dorset. Similar specimens occur in the Corallian rocks of Dorset, and these are likewise slightly smaller than the type specimen.

Bullopora rostrata Quenstedt

Text-fig. 1 (3)

- 1858 *Bullopora rostrata* Quenstedt, p. 580, pl. 73, fig. 28.
 1935 *Bullopora rostrata* Quenstedt; Macfadyen, p. 18, pl. 1, figs. 23, 24.
 1941 *Bullopora rostrata* Quenstedt; Macfadyen, p. 25, pl. 1, figs. 13–17.
 1952 *Bullopora rostrata* Quenstedt; Barnard, p. 348, fig. B, 8.
 1953 *Bullopora rostrata* Quenstedt; Barnard, p. 192.

Material. Five specimens from Knapwell.

Description. The adherent, imperforate, white, opaque test consists of up to twelve chambers. It starts with a loose coil of three hemi-ellipsoidal chambers and this is followed by a meandrine series of chambers which are hemi-ellipsoidal or irregular in shape at first, but which soon become elongate and bulbous or club-shaped. After the initial part there is no increase in the size of the chambers. The aperture is terminal, simple, semicircular. All the specimens were attached to lamellibranch shell fragments.

Dimensions. Greatest width of the chambers, 0.09–0.15 mm.

Remarks. *Bullopora rostrata* was described by Quenstedt from the Oxfordian (*Impressa* Beds) of Reichenbach, Saxony, and Macfadyen (1941) has given a long synonymy for this species. Unfortunately, there seems to be some confusion in the literature between a perforate and an imperforate species of adherent foraminifer which are broadly isomorphous in gross morphology, and it is not felt to be advisable to attempt a lengthy synonymy at this time. Forms which appear to be similar to the Ampthill Clay material are reported widely in Europe from the Lower Lias to the Oxfordian, but the only non-European record appears to be that of Macfadyen (1935) from probable Argovian, British Somaliland. Some of the Lias specimens differ slightly from the Ampthill form in having more slender chambers.

Family TROCHAMMINIDAE

Genus TROCHAMMINA Parker and Jones 1859

Trochammina squamata Jones and Parker

Text-fig. 1 (6)

- 1860a *Trochammina squamata* Jones and Parker, p. 304.
 1890 *Trochammina squamata* Jones and Parker; Haeusler, p. 65, pl. 10, figs. 27–29, 40.
 1937 *Trochammina squamata* Jones and Parker; Bartenstein and Brand, p. 190, pl. 6, fig. 41; pl. 11b, fig. 29; pl. 15c, figs. 22a, b.
 1959 *Trochammina squamata* Jones and Parker; Lloyd, p. 316, pl. 54, fig. 29; text-fig. 5a.

Material. Three specimens from Mepal.

Dimensions. Greatest diameter of the tests, 0.28, 0.29, 0.31 mm.

Remarks. There is nothing to add to previous descriptions. The Upper Jurassic forms which have been ascribed to this species are indistinguishable from the original material which was described by Jones and Parker from the Recent, off the island of Crete.

Family LAGENIDAE

Genus LENTICULINA Lamarck 1804

Forms which here are placed in the genus *Lenticulina* would be called *Cristellaria* by some authors, but Glaessner (1945) considers that *Cristellaria* Lamarck 1816 is probably invalid. He states that it is probably a synonym of one or more of the many names given by Montfort in 1808. Most of these in turn are probably synonyms of *Lenticulina*. Cushman (1950) states that 'in many species it is very difficult to separate *Robulus* from *Lenticulina* and it may be best as a practical matter to drop *Robulus* and use *Lenticulina* for both'. *Cristellaria* Lamarck 1816 is regarded by him as a synonym of *Robulus* Montfort 1808.

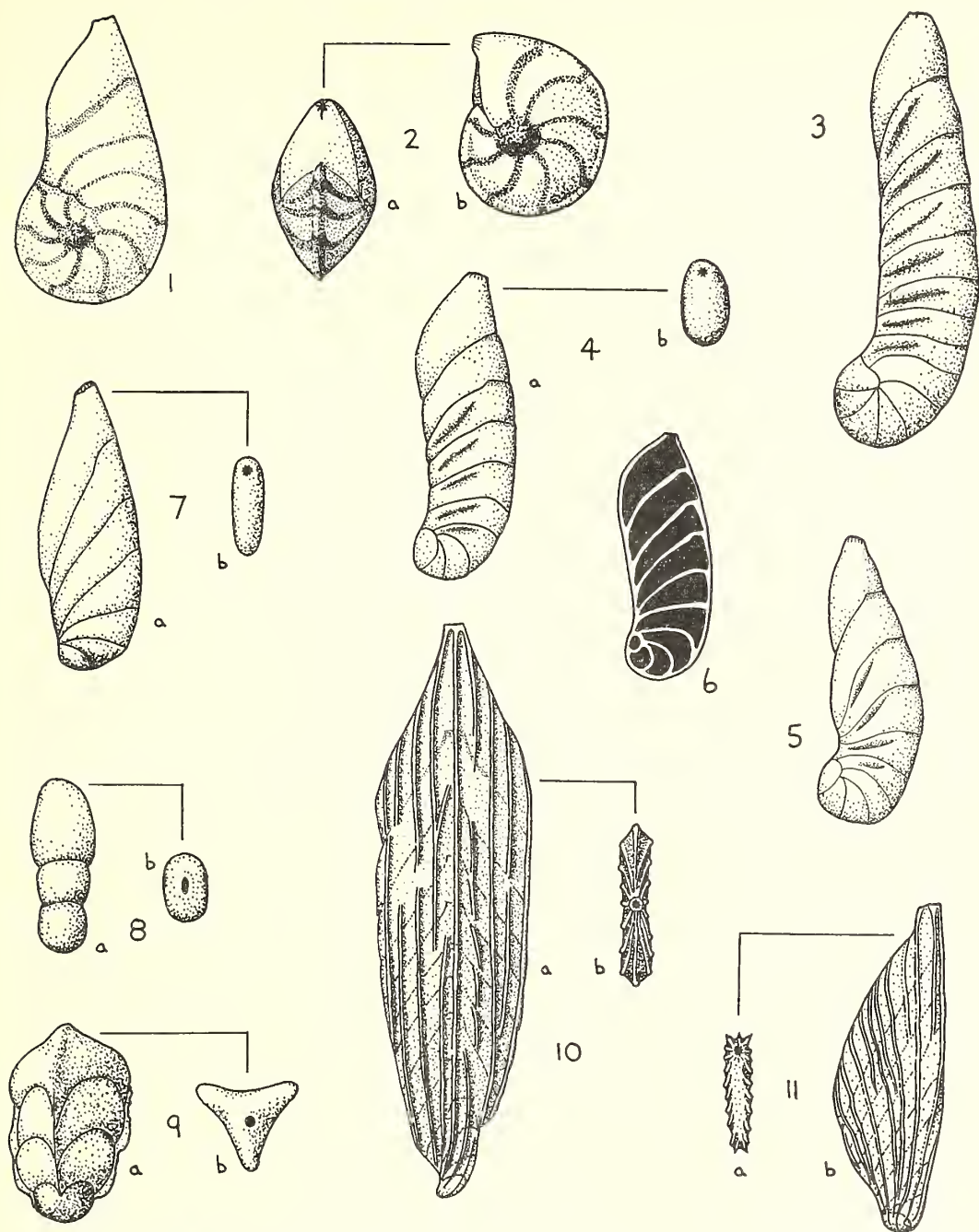
Lenticulina münsteri (Roemer)

Text-fig. 2 (1), (2)

- 1839 *Robulina münsteri* Roemer, p. 48, pl. 20, figs. 29a, b.
- ?1839 *Robulina gibba* Roemer, p. 47, pl. 20, figs. 30a, b.
- ?1865 *Cristellaria semiexpleta* Schwager, p. 134, pl. 7, figs. 1a, b.
- 1867 *Cristellaria sowerbyi* Schwager, p. 660, pl. 34, fig. 18.
- 1867 *Cristellaria vulgaris* Schwager, p. 661, pl. 34, fig. 19.
- 1884 *Cristellaria sowerbyi* Schwager; Deceke, p. 50, pl. 2, fig. 18.
- 1884 *Cristellaria rotulata* (Lamarck); Jones, pp. 765, 767, 770, pl. 34, fig. 9.
- ?1886 *Cristellaria sowerbyi* Schwager; Deceke, p. 34, pl. 2, figs. 34, 34a.
- 1892 *Cristellaria cultrata* (Montfort); Crick and Sherborn, p. 70, pl., figs. 13a, b.
- ?1904 *Cristellaria rotulata* (Lamarck); Chapman, p. 192, pl. 22, fig. 9.
- 1932 *Lenticulina münsteri* (Roemer); Paalzow, p. 101, pl. 5, figs. 23, 24; pl. 6, figs. 1, 2.
- 1935 *Cristellaria münsteri* (Roemer); Macfadyen, p. 13, pl. 1, figs. 10a, b.
- 1937 *Cristellaria* (*Lenticulina*) *münsteri* (Roemer); Bartenstein and Brand, p. 174, pl. 3, figs. 30a, b; pl. 4, figs. 69a-c; pl. 6, figs. 34a-d; pl. 9, figs. 49a-e; pl. 10, figs. 38a, b; pl. 11A, figs. 13a-d; pl. 11B, figs. 19a-d; pl. 12A, figs. 16a, b; pl. 12B, figs. 15a-e; pl. 13, fig. 36; pl. 14B, figs. 14a-c; pl. 14C, figs. 13a, b; pl. 15A, figs. 34a-c; pl. 15C, figs. 19a-c.
- 1938 *Cristellaria* (*Lenticulina*) *varians* Bornemann; Wicher, pl. 20, fig. 5.
- 1941 *Cristellaria münsteri* (Roemer); Macfadyen, p. 31, pl. 2, figs. 23a, b.
- 1950b *Lenticulina münsteri* (Roemer); Barnard, p. 7, pl. 2, fig. 1.
- 1952 *Lenticulina münsteri* (Roemer); Barnard, p. 339, fig. B, 5.
- 1953 *Lenticulina münsteri* (Roemer); Barnard, p. 185, fig. A, 10.
- 1954 *Lenticulina münsteri* (Roemer); Bielecka and Pozaryski, pp. 33, 165, pl. 4, figs. 12a, b.

Material. Thirty-eight specimens from Knapwell; 55 from Mepal.

Description. The test is composed of one and a half whorls which are at first involute, but which may become evolute. In some individuals there are about ten chambers in the last whorl, and the thickness of the test is one-third to almost one-half of the greatest diameter of the test. The periphery is subangular to carinate, smoothly curving or polygonal. Sometimes the thickness of the test wall at the periphery gives the appearance of a keel in side view when the test is in fact not carinate. The umbilicus usually has an infilling of clear calcite which is flush with the surface of the test, but some-



TEXT-FIG. 2. (1) *Lenticulina münsteri* (Roemer). Mepal. $\times 40$. (2)a, b. *Lenticulina münsteri* (Roemer). Knapwell. $\times 40$. (3) *Lenticulina suprajurassica* sp. nov. Holotype. Mepal. $\times 40$. (4)a, b, (5) *Lenticulina suprajurassica* sp. nov. Paratypes. Mepal. $\times 40$. (6) *Lenticulina suprajurassica* sp. nov. Longitudinal section. Mepal. $\times 40$. (7)a, b. *Planularia fraasi* (Schwager). Knapwell. $\times 75$. (8)a, b. *Lingulina nodosaria* Reuss. Knapwell. $\times 75$. (9)a, b. *Tristix oolithica* (Terquem). Knapwell. $\times 75$. (10)a, b. *Falsopalmula anceps* (Terquem). Knapwell. $\times 40$. (11)a, b. *Citharina serratocostata* (Gümbel). Mepal. $\times 40$.

times there are raised umbilical bosses which give the test a globose appearance. The sutures are limbate, flush, or raised into low ribs, and they curve with the convex side towards the aperture, but with a sharp recurvature at the periphery. The proloculum is spherical.

Individuals which uncoil have up to five chambers arranged in a straight or curving terminal series, and the later ones of these may be inflated. In this portion the sutures slope back strongly or weakly towards the proloculum at the non-apertural margin. They become less limbate, ribs which may be present earlier in the test now disappear, and finally the sutures become depressed.

The aperture is marginal, terminal, radiate, sometimes on a small extension of the final chamber.

Dimensions. Length of the largest uncoiling specimen, 1.3 mm. In completely coiled individuals, the greatest diameter of the test is usually about 0.7 mm.

Remarks. *Lenticulina münsteri* was originally described from the Lower Cretaceous (Hils) of Schöppenstedt, north Germany, but it has subsequently been recorded throughout the Jurassic of Europe. Outside Europe, Chapman (1904) illustrates a form which is possibly the same species from the Jurassic of Western Australia, and Macfadyen (1935) has recorded it from probable Argovian, British Somaliland. The characteristics of the form which most authors refer to Roemer's '*Robulina münsteri*' are clear, but the type reference of the species is far from satisfactory.

Lenticulina suprajurassica sp. nov.

Text-fig. 2 (3), (4), (5), (6)

?1870a *Cristellaria hybrida* Terquem (pars), p. 441, pl. 14, figs. 14a, b, 17, 19.

?1954 *Lenticulina priuna* (d'Orbigny); Bielecka and Pozaryski, pp. 38, 170, pl. 5, figs. 19a, b.

1955 *Lenticulina (Astacolus) priuna frauconica* (Gümbel); Seibold and Seibold, p. 109, text-figs. 3k, l, pl. 13, fig. 6.

Material. Seven specimens from Knapwell; 58 from Mepal.

Description. The test has an initial coil of four to six chambers, followed by a curving series of up to eight chambers. It is compressed, the thickness of the test being about half the width. The initial coil is globose, evolute, with a subangular periphery which becomes rounded later. The first two or three sutures are flush, curving, but subsequent sutures are depressed at the non-apertural margin and flush or raised into low ribs at the sides and apertural margin. In the uncoiled part of the test, the sutures are at first transverse, but rapidly become oblique, sloping towards the initial end at the non-apertural margin. The uncoiled chambers are characteristically more than twice as broad as they are high, and in many specimens they are ornamented by a broad groove on each side of the test. This ornament does not appear to be a secondary effect caused by crushing. The end chamber is usually inflated, but is little differentiated from the preceding chambers. The aperture is terminal, marginal, radiate, and is sometimes on a small projection of the final chamber.

Dimensions. Length, up to 1.66 mm.; usually about 0.8–1.1 mm.

Remarks. This species is distinguished from most other uncoiling *Lenticulinae* in the

Jurassic by its brief evolute coil, the lowness of the chambers in the uncoiled part, and the typically curvilinear rather than rectilinear form of the uncoiled part.

Some of the many forms from the Bajocian of eastern France which Terquem has grouped together as *Cristellaria hybrida* may belong here. Other similar forms have been recorded from the Kimmeridgian and Portlandian of Poland (Bielecka and Pozaryski 1954), but they have a coil of about ten chambers, and the curvilinear chambers are not so low as those of the Ampthill Clay forms. The Seibold's form from the Oxfordian of south Germany appears to be very close to the Ampthill Clay specimens. The Brady collection of foraminifera at the British Museum (Natural History) includes specimens from the Kimmeridge Clay which are identical with the Ampthill material.

Genus PLANULARIA Defrance 1824

Planularia fraasi (Schwager)

Text-fig. 2 (7)

- non 1854 *Cristellaria protracta* Bornemann, p. 39, pl. 4, figs. 27a, b.
- 1865 *Cristellaria fraasi* Schwager (non Gümbel, 1871), p. 123, pl. 5, fig. 10.
- 1865 *Cristellaria lanceolata* Schwager, p. 130, pl. 6, fig. 13.
- 1952 *Planularia protracta* (Bornemann); Barnard, p. 343, figs. C, a-d.
- 1953 *Planularia protracta* (Bornemann); Barnard, p. 186, fig. A, 4.
- 1956 *Lenticulina* (*Planularia*) *lanceolata* (Schwager); Seibold and Seibold, p. 113, text-figs. 6p, q; pl. 7, fig. 6.

Material. Five specimens from Knapwell.

Description. The compressed, lanceolate test lacks ornament and is composed of about eight chambers. The length of the test is two to three times its greatest width, and the thickness is about one-third of the width. The initial coil is variable and irregular in form and has been discussed by Barnard (1952). The aperture is radiate.

Dimensions. Length, 0.41–0.57 mm.

Remarks. The stylized illustrations and generalized descriptions given by many of the older authors make difficult the construction of an adequate synonymy for these forms. Many of the smooth Upper Jurassic *Planulariae* have been referred to *Planularia protracta*, described by Bornemann from the Lower Lias of Göttingen, but the Upper Jurassic forms appear to differ from this in several ways. They are not so elongate, the initial coil is better developed and is more irregular in form, and the later chambers extend more strongly back towards the proloculum at the non-apertural margin. Schwager's original description of *Planularia fraasi* was from the Oxfordian of Franconia.

Genus NODOSARIA Lamarck 1812

Nodosaria sowerbyi Schwager

- 1867 *Nodosaria sowerbyi* Schwager, p. 656, pl. 34, fig. 8.

Material. One specimen from Knapwell.

Dimensions. Length, 0.63 mm.

Remarks. A single specimen composed of six chambers is referred to this species which

Schwager described from the *sowerbyi* Zone (Bajocian) of Aargau, Switzerland. The sutures of the Ampthill Clay specimen are slightly less constricted than are those of the Swiss Bajocian form.

Genus TRISTIX Macfadyen 1941

Tristix oolithica (Terquem)

Text-fig. 2 (9)

1886 *Tritaxia oolithica* Terquem, p. 60, pl. 7, figs. 5a, b.

1937 *Trifarina oolithica* (Terquem); Bartenstein and Brand, p. 186, pl. 11B, fig. 26; pl. 15B, figs. 2a-c.

Material. One specimen from Knapwell.

Description. The test is triangular in cross-section, smooth, and consists of four chambers. Except on the first and last chambers, there is a prominent keel at the test margins. The aperture appears to be simple.

Dimensions. Length, 0.39 mm.

Remarks. Comparison of the Ampthill Clay specimen with the many specimens which I have found in rocks of comparable age on the Dorset coast indicates that this specimen is megalospheric. Terquem's original description of the species was from the Fuller's Earth of Warsaw.

Genus LINGULINA d'Orbigny 1826

Lingulina nodosaria Reuss

Text-fig. 2 (8)

1863 *Lingulina nodosaria* Reuss, p. 59, pl. 5, figs. 12a, b.

1953 *Lingulina* cf. *laevissima* (Terquem); Barnard, p. 186, figs. B, 8a, b.

Material. Three specimens from Knapwell; one from Mepal.

Description. The smooth rectilinear test consists of three to six chambers and its thickness is about two-thirds of the breadth. The margins are lobulate. The proloculum is subspherical, and subsequent chambers increase in size slowly and regularly. The sutures are depressed, arcuate. The apertural chamber is compressed-pyriform and the aperture is central, terminal, elliptical. No microspheric forms were found.

Dimensions. Lengths of the specimens, 0.38, 0.39, 0.45, and 0.5 mm.

Remarks. Reuss described this species from the Lower Cretaceous of north Germany. *Lingulina laevissima* (Terquem), described from the Lower Lias of Moselle, eastern France, differs in having sutures which are straight, transverse, except at the latest stage, and in being not indented at the margins until the final two chambers. Some of the forms which have been referred to Terquem's species are fairly similar to the Ampthill Clay specimens, but they commonly differ in being highly compressed. The form recorded by Barnard (1953) is compressed, but is otherwise very similar to my form and is considered to be conspecific with it.

Genus CITHARINA d'Orbigny 1839, emend. Marie 1938

It is not possible to draw a precise boundary between this genus and *Vaginulina*, but it seems to be useful to retain the name *Citharina* for compressed, triangular forms which have no coil. Glaessner (1945) considers that *Citharina* should be distinguished from *Vaginulina*, and Marie (1938) selected *Vaginulina striatula* Roemer 1842 as the genotype.

Citharina serratocostata (Gümbel)

Text-fig. 2 (11)

- 1862 *Marginulina serratocostata* Gümbel, p. 222, pl. 4, figs. 23a, b.
1862 *Marginulina flabellata* Gümbel, p. 223, pl. 4, figs. 24a-c.
1867 *Cristellaria lepida* Schwager, p. 657, pl. 34, fig. 9.
1890 *Vaginulina harpa* Roemer var. *furcata* Wisniewski, p. 209, pl. 9, fig. 6.
cf. 1917 *Vaginulina flabellata* (Gümbel); Paalzow, p. 237, pl. 45, figs. 5, 6, 7.
1921 *Vaginulina harpa* Roemer; Neaverson, p. 463, pl. 9, fig. 7.
1933 *Vaginulina lepida* (Schwager); Wickenden, p. 163, pl. 1, figs. 15, 16.
1937 *Vaginulina harpa* Roemer; Bartenstein and Brand, p. 163, pl. 14b, fig. 7; pl. 14c, fig. 10; pl. 15A, figs. 24a, b; pl. 15c, figs. 12a-d.
1950 *Vaginulina catanlaca* Loeblich and Tappan, p. 54, pl. 14, figs. 22, 23a, b.
1950 *Citharina entypomatus* Loeblich and Tappan, p. 57, pl. 15, figs. 1-12.
1950 *Vaginulina lancea* Lalicker, p. 16, pl. 3, fig. 3.
1950 *Vaginulina pola* Lalicker, p. 17, pl. 3, figs. 4a, b.
1950 *Vaginulina cetra* Lalicker, p. 17, pl. 3, fig. 5.
1953 *Citharina* cf. *serratocostata* (Gümbel); Barnard, p. 190, figs. A, 11a-e.
1954 *Vaginulina proxima* (Terquem); Bielecka and Pozaryski, pp. 44, 175, pl. 6, fig. 25.

Material. Seven specimens from Knapwell; thirty from Mepal.

Description. The test is compressed, triangular, broad to elongate, and composed of seven to sixteen chambers. The thickness of the test is one-third to a quarter of its width. The margins diverge rapidly at first but are frequently subparallel later. The apertural margin is entire, but the non-apertural margin is often lobulate especially later on. The proloculum is spherical or ellipsoidal, inflated or flush. A loose initial coil with triangular chambers is followed by a series of elongate, parallel sided, curving chambers with the greatest curvature near the apertural margin. The final chambers are straight, curved only at the apertural margin. The sutures may be depressed at the non-apertural margin, but otherwise they are flush. There is an ornament of coarse branching ribs. The apertural face is rectangular, smooth except at the margins where the terminations of the ribs produce frilling. The aperture is marginal, terminal, radiate or simple, often on a grooved neck from the last chamber.

Dimensions. Length, up to 2.0 mm.; usually about 1.0 mm.

Remarks. Many compressed, triangular, ribbed forms have been recorded from the Jurassic and Cretaceous under a variety of names, but the stylized mode of illustration adopted by many of the earlier authors has made it impossible to construct an entirely satisfactory synonymy for the Ampthill Clay specimens from the literature alone. In particular, many forms illustrated by Terquem (1868, pls. 1-7) from the Middle Jurassic of the Moselle Department are probably conspecific with the Ampthill specimens, but

any treatment of these without recourse to the original material would be inadequate or useless.

Citharina serratocostata was described by Gümbel from the lower Oxfordian of Streitberg, south Germany. The type specimen appears to be extremely narrow and the ribs are shown in the figure as if they do not branch, but there is little doubt that this belongs to the same species as the Ampthill forms. Some authors have ascribed to *Vaginulina harpa* Roemer forms which I regard as being conspecific with Gümbel's species, and it is possible that the Ampthill specimens should also be placed in this species. On the other hand, *Vaginulina harpa*, described by Roemer (1840-1) from the Lower Cretaceous (Hilsthon) of north Germany, was unsatisfactorily figured by the original author and it has been variously interpreted.

Forms which are the same as the Ampthill Clay species occur widely in the Middle and Upper Jurassic of Europe. They have also been recorded from the Jurassic of North America under different names. They occur in approximately the Bajocian of Saskatchewan and Alberta (Wickenden 1933); the Ellis group, approximately Bathonian, of Montana (Lalicker 1950); and the Redwater Shale, Upper Jurassic, of South Dakota (Loeblich and Tappan 1950a).

Genus FALSOPALMULA Bartenstein 1948

Falsopalmula anceps (Terquem)

Text-fig. 2 (10)

1870b *Flabellina anceps* Terquem, p. 223, pl. 23, figs. 25a, b.

1870b *Flabellina semi-involuta* Terquem (pars), p. 225, pl. 23, fig. 30; pl. 24, figs. 6-10.

1937 *Flabellina mölleri* Uhlig; Bartenstein and Brand, p. 169, pl. 15A, figs. 27a-c; pl. 15C, figs. 13a, b.

1948 *Falsopalmula semi-involuta* (Terquem); Bartenstein, p. 130, pl. 2, figs. 16-18.

1950 *Fronicularia spatha* Lalicker, p. 17, pl. 3, figs. 6a-d.

1950 *Citharinella exarata* Loeblich and Tappan, p. 58, pl. 16, figs. 4-8.

Material. Thirteen specimens from Knapwell; four from Mepal.

Description. The test is extremely variable in form, but it is usually lanceolate or lozenge-shaped, compressed, and consisting of eight to thirteen chambers. In most specimens, the thickness of the test is about one-quarter of the width, but the length varies widely. The margins of the test are entire at first, later becoming lobulate. The proloculum is spherical or ellipsoidal, usually flush, and in most specimens is followed by a loose coil of three to six chambers. The coil is succeeded by chevron-shaped chambers, the first of which partly embraces the coil at the peripheries. Except sometimes for the first one, the chevron-shaped chambers are bilaterally symmetrical. The sutures are flush. There is an ornament of coarse ribs, some of which branch. The aperture is central, terminal, radiate, on a neck from the last chamber. In the earlier growth stages, it is peripheral.

Dimensions. Length, 0.46-3.04 mm.

Remarks. *Falsopalmula anceps* was described by Terquem from the *parkinsoni* Zone (Bajocian) of Fontoy, Moselle, eastern France. The striate varieties of a group of specimens from the same beds which Terquem described as *Flabellina semi-involuta*

show a similar variation to that of the Ampthill specimens and should probably be placed in the same species.

Two North American forms appear to be conspecific with the Ampthill Clay specimens. *Citharinella exarata*, described from the Redwater Shale (Upper Jurassic) of South Dakota, seems to differ only in its slightly greater size; and *Fronicularia spatha*, from the Ellis group, Sawtooth member (approximately Bathonian) of Montana, differs slightly in having an ornament of ribs which are discontinuous, but is otherwise closely similar.

The generic placing of this species is made difficult by the transgression of the variation across the boundaries between widely accepted genera, but the median and most abundant forms fall within *Falsopalmula* Bartenstein.

Family EPISTOMARIIDAE

Genus VOORTHUYSENIA Hofker 1954

Voorthuysenia tenuicostata (Bartenstein and Brand)

Text-fig. 1 (7)

- ?1860b *Rotalia elegans* d'Orbigny; Jones and Parker, p. 452, pl. 20, fig. 46.
 1898 *Pulvinulina elegans* (d'Orbigny); Chapman, p. 6, pl. 1, figs. 8a-c.
 1898 *Pulvinulina caracolla* (Roemer); Chapman, p. 7, pl. 1, figs. 9a-c.
 1932 *Epistomina caracolla* (Roemer); Paalzow, p. 142, pl. 11, figs. 12-14.
 1935 *Epistomina elegans* (d'Orbigny); Macfadyen, p. 16, pl. 1, figs. 20a, b, c.
 1951 *Epistomina tenuicostata* Bartenstein and Brand, p. 327, pl. 12A, figs. 325a-c.
 1953 *Epistomina* cf. *elegans* (d'Orbigny); Barnard, p. 193, figs. A, 7a-c.
 1954 *Voorthuysenia tenuicostata* (Bartenstein); Hofker, p. 186, figs. 19a-g.

Material. Seventy-five specimens from Knapwell; 108 from Mepal.

Description. The test is biconvex, trochoid, consisting of $1\frac{1}{2}$ to $2\frac{1}{2}$ whorls, with seven or eight chambers in the last whorl. The periphery is usually entire, but is sometimes weakly lobulate. The dorsal side is usually less strongly convex than the ventral. The height of the test is one-half to two-thirds of the greatest diameter. On the dorsal side, the whole spire is visible, and the slope of the spire may be either concave or convex. Frequently, there is a large dorsal boss which obscures the earlier chambers. The sutures are limbate, and they curve backwards from the inner margin to join the peripheral margin smoothly. On the ventral side, only the last whorl is visible; the sutures are limbate, radial, usually straight, and sometimes raised; the outlines of what are presumably secondary apertures are seen near the periphery on each chamber. The final whorl is sometimes excavated parallel to the periphery on each side of the test. The apertural face is triangular. The apertural chamber is broken in all specimens and the aperture was not seen.

The direction of the coiling may be dextral or sinistral, as tabulated below:

	Number of dextral specimens	Number of sinistral specimens	Number of specimens in which the direction of coiling is obscure
Knapwell	16	55	4
Mepal	34	67	7

Dimensions. Greatest diameter of the test, up to 0.59 mm.; usually it is 0.38-0.42 mm.

Remarks. This species was described by Bartenstein and Brand from the Valendisian of north-west Germany, but Hofker (1954) records it also from the Malm. An apparently similar form was recorded by Jones and Parker (1860*b*) from clay at Chellaston, Derbyshire, which they ascribed to the Upper Trias, but which Crick and Sherborn (1892), Issler (1908), and Macfadyen (1941) consider more likely to be Upper Liassic. Some of the Ampthill Clay specimens have thick, raised sutures which coalesce at the centre on both the dorsal and ventral sides; they are similar to *Voortluysenia pachyderma* Hofker from the Middle Jurassic, but in the Ampthill these forms grade into typical *V. tenuicostata*.

CONCLUSIONS

Of the seventeen species of foraminifera recorded from the Ampthill Clay, eight are Lagenids. This apparent predominance of the Lagenidae is less marked when a comparison is made on the basis of numbers of individual specimens which occur in the faunas. In the Knapwell fauna, 75 of the specimens found are Lagenids, 75 are *Voortluysenia tenuicostata* (Bartenstein and Brand), and 73 are other forms, principally *Amnobaaculites coprolithiformis* (Schwager). In the Mepal fauna, the numbers are 148 Lagenids, 108 *V. tenuicostata*, and 51 others. The composition of the faunas of the two samples is shown in the table.

Distribution of the species of foraminifera

	Knapwell	Mepal
<i>Cribrostomoides canui</i> (Cushman)		×
<i>Amnobaaculites agglutinans</i> (d'Orbigny)		×
<i>Amnobaaculites coprolithiformis</i> (Schwager)	×	×
<i>Amnobaaculites</i> cf. <i>reophaciformis</i> Cushman		×
<i>Bigenenerina</i> cf. <i>nodosaria</i> d'Orbigny		×
<i>Bullopore globulata</i> Barnard	×	
<i>Bullopore rostrata</i> Quenstedt	×	
<i>Trochammmina squamata</i> Jones and Parker		×
<i>Lenticulina münsteri</i> (Roemer)	×	×
<i>Lenticulina suprajurassica</i>	×	×
<i>Planularia fraasi</i> (Schwager)	×	
<i>Nodosaria sowerbyi</i> Schwager	×	
<i>Tristix oolithica</i> (Terquem)	×	
<i>Lingulina nodosaria</i> Reuss	×	×
<i>Citharina serratocostata</i> (Gümbel)	×	×
<i>Falsopalmula anceps</i> (Terquem)	×	×
<i>Voortluysenia tenuicostata</i> (Bartenstein and Brand)	×	×

The Knapwell fauna includes a greater variety of Lagenids, but only one species of arenaceous foraminifer, while the Mepal fauna has fewer species of Lagenids, but a more diverse set of arenaceous forms.

Considering the Knapwell and Mepal foraminiferal faunas together, the assemblage is more closely comparable to that of the Nothe Clay in the Dorset Corallian Beds than

to the fauna of any other formation. All the Ampthill Clay species except *Amniobaculites* cf. *reophaciformis* Cushman occur in the Nothe Clay, whereas the Glos Oolite Series of Dorset, more comparable in age to the Ampthill Clay, lacks several of the more characteristic Ampthill species including *Lenticulina suprajurassica* sp. nov. and *Voorthuysenia tenuicostata* (Bartenstein and Brand).

In general, the Ampthill Clay foraminiferal fauna is quite similar to the foraminiferal faunas of the Corallian Beds of Dorset, but the relative abundances of the species present in the Ampthill are distinctive. *Voorthuysenia tenuicostata* (Bartenstein and Brand) is the most important species in both the Knapwell and the Mepal samples, but in the Corallian of Dorset it is numerous only at restricted levels in the Nothe and Ringstead Waxy Clays. *Lenticulina suprajurassica* sp. nov. is common in the Ampthill Clay but scarcely represented in Dorset; while *Amniobaculites coprolithiformis* (Schwager) is extremely abundant in the upper Oxford Clay and lower Corallian of Dorset but is less abundant in the Ampthill Clay. On the whole, nevertheless, the foraminifera of the Ampthill Clay samples described in this paper are typical of the English Corallian Beds and of the Oxfordian stage.

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A MIDDLE DEVONIAN INADUNATE CRINOID FROM WEST SOMERSET, ENGLAND

by B. D. WEBBY

ABSTRACT. *Decadocrinus oaktrovensis* sp. nov., is described from Middle Devonian (Givetian) strata near Timberscombe, west Somerset, in the lower half of the Ilfracombe Beds.

ALTHOUGH disarticulated crinoid ossicles are common in marine Devonian strata of north Devon and west Somerset, reasonably complete crinoids are exceedingly rare. Whidborne (1896–8) described a number of crinoids from the Pilton Beds, but none has previously been described from older Devonian rocks in north Devon and west Somerset.

A small outcrop at a sharp bend on the private road between the main highway (A396) and Oaktrow farmhouse (National Grid Reference SS941404), two miles south-west of Timberscombe, yielded a large number of good specimens, all belonging to a single crinoid species, *Decadocrinus oaktrovensis* sp. nov. The specimens occur as moulds in weathered, light-brown, originally calcareous siltstone. Nearby, in the disused Oaktrow quarries (SS939402) stratigraphically only a few tens of feet above or below the crinoidal horizon, a fauna of brachiopods, lamellibranchs, gastropods, Bryozoa, and crinoid ossicles has been collected. Two of the brachiopods have been identified as *Spinocyrtia ascendens* (Priestersbach 1935), a Givetian species in Germany (Priestersbach 1942), and *Thomassaria gibbosa* Vandercammen 1956, which occurs in upper Givetian and Frasnian strata in Belgium. A description of this fauna and the stratigraphy of the area will be published later.

SYSTEMATICS

The classification followed is that given by Moore and Laudon (1943). Numbers of specimens catalogued in the Bristol University Geology Department Collection are prefixed BU.

Subclass INADUNATA Wachsmuth and Springer

Order CLADOIDEA Moore and Laudon

Suborder DENDROCRINOIDEA Bather

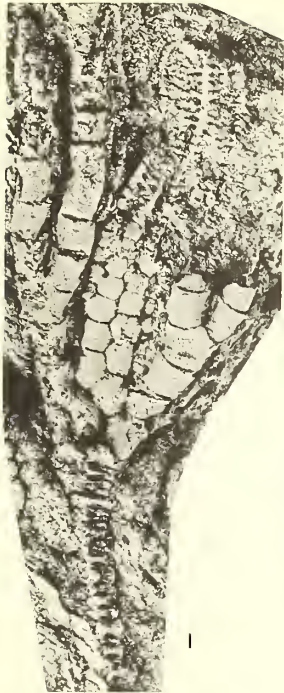
Family SCYTALOCRINIDAE Moore and Laudon 1943

Genus DECAOCRINUS Wachsmuth and Springer 1879

EXPLANATION OF PLATE 67

All figures $\times 4$; from latex (Revutex) casts of external moulds.

Figs. 1–7 *Decadocrinus oaktrovensis* sp. nov. 1, Holotype, BU 15358, posterior view, showing arrangement of plates in the posterior interradius and the proximal part of the anal sac. 2, Paratype, BU 15359, left lateral view, showing the arrangement of plates in the dorsal cup, small infrabasals, large basals and radials, and the isotomous branching of arms on the second primibrach. 3, Paratype, BU 15360, right posterolateral view, showing large recurved, plicated, anal sac. 4, Paratype, BU 15362, right posterolateral view, showing recurved, plicated, anal sac. 5, BU 15364, view of stem, showing alternate high nodals and low internodals with a few nodals bearing cirri. 6, Paratype, BU 15365, view of arm, showing single isotomous branching on the second primibrach, and pinnules on alternate secundibrachs. 7, Paratype, BU 15367, view of pinnules.



WEBBY, Devonian crinoid

Type species (by original designation, Wachsmuth and Springer 1879, pp. 332, 342-3). *Poteriocrinites* (*Scaphiocrinus* or *Graphiocrinus*) *scalaris* Meek and Worthen 1869, pp. 137, 139, 145-6.

Discussion. The genus *Decadocrinus* has a Devonian and Carboniferous time-range according to Moore (*in* Shimer and Shrock 1944). The North American Devonian species have been described by Goldring (1923; 1954), Laudon (1936), and Kier (1952). W. E. Schmidt (1941) considered that some of the species described by Goldring in 1923 should be assigned to a new genus, because they have laterally visible infrabasals. However, in the original diagnosis of *Decadocrinus*, Wachsmuth and Springer (1879, p. 342) stated that infrabasals are 'small, frequently hidden from view in the concave base'. Clearly, this statement implies that species with visible infrabasals can be included in the genus *Decadocrinus*. Schmidt, in his belief that the presence of laterally visible infrabasals was contrary to the original diagnosis of Wachsmuth and Springer, introduced *Denariocrinus* for those Devonian forms with laterally visible infrabasals, three to four anal plates in the cup, and each arm with a single forking on or above the second primibrach. The type species, *Denariocrinus ferula* W. E. Schmidt, is from the Eifelian of Germany. As the diagnosis of *Decadocrinus* includes the same characters, it seems better to regard *Denariocrinus* as a synonym of *Decadocrinus*, at least until further specimens are obtained from Europe, North America, and elsewhere for comparative study.

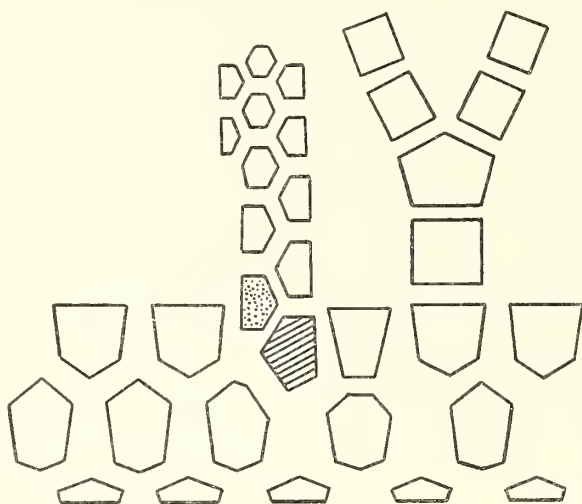
Decadocrinus oaktrovensis sp. nov.

Plate 67; text-fig. 1

Diagnosis. A small species of *Decadocrinus* with the dorsal cup a little wider than high; basals convex and depressed at sutures, higher than wide; brachials smooth, usually slightly higher than wide.

Description. Dorsal cup small, conical, sutures depressed especially between the basals. Infrabasals small, pentagonal, twice as wide as high. Basals hexagonal, except for heptagonal posterior basal and right posterior basal; convex, slightly higher than wide. Radials convex, similar in size to basals, pentagonal, except right posterior radial which is trapezoidal in outline and slightly smaller than the other four; radials as wide as high; facets curved and occupying full width of radials. Primibrachs two, the first quadrangular, as wide as high; the second (axillary) pentagonal, slightly wider than high; a single isotomous branching of each arm; arms long, slender, tapering gradually towards the distal end, observed to a length of 24 mm. above axillary; thirty-seven secundibrachs observed in one paratype (BU 15365); brachials uniserial, smooth, rounded, pinnulate, usually slightly higher than wide. Pinnules borne on every second secundibrach; pinnule segments higher than wide, oval in section. Posterior interradius with pentagonal radianal at the level of the radials and adjacent to right posterior radial, a little smaller than basals; anal X pentagonal, slightly smaller than radianal. Anal X and radianal support large, recurved, anal sac; a row of anal tube plates rests on both anal X and radianal, and gradually decreases in size distally; a further row of plates is seen above the second tube plates; in the distal recurved part of the sac three to four rows of small plates are observed; each row of plates bears a strong central ridge with horizontal

flutings giving the upper part of the anal sac a plicated appearance; anal opening not seen. Stem observed to a length of 45 mm.; pentagonal to slightly stellate in the proximal 10 mm., distally round; columnals near cup low, slightly stellate with swollen corners, but distally columnals are round and alternate between high nodals and low internodals;



TEXT-FIG. 1. Diagram showing the arrangement of plates in the dorsal cup, the proximal part of the anal sac, and the proximal part of an arm of *Decadocrinus oaktrovensis* sp. nov. Five infrabasals, five basals, five radials, a radianal (shown ruled), and anal X (shown stippled) in the dorsal cup. Arm with a single isotomous branching on the second primibrach. Proximal part of anal sac with two rows of tube plates resting on radianal and anal X respectively; above the second tube plates a third row of plates visible.

nodal columnals bear long, slender, tapering cirri; cirri composed of numerous thin, disk-like segments.

Dimensions (in mm.)

	<i>Holotype</i>	<i>Paratypes</i>				
	BU 15358	BU 15359	BU 15360	BU 15361	BU 15362	BU 15363
Hc	3.0	2.8	3.1	2.7	4.0	2.7
Had	6.4	..	6.1	..	6.2	..
Hah	13.0	..	16.5	..	11.2	..
Wcr	4.8	4.1	4.2	3.6	3.5	4.7
Web	2.1	2.0	2.2	2.0	1.9	1.8

Hc, height of dorsal cup; Had, height of anal sac from base of radianal to distal recurved tip of anal sac; Hah, height of anal sac from base of radianal to greatest height of sac; Wcr, width of dorsal cup at the level of the radial facets; Web, width of dorsal cup at the base of the dorsal cup.

Holotype. BU 15358, Pl. 67, fig. 1. *Paratypes.* BU 15359–67.

Remarks. *Decadocrinus oaktrovensis* resembles both the Middle Devonian North American forms *D. stewartae* Kier (1952, pp. 73–74) from the Silica Formation of Ohio,

and *D. wrightae* Goldring (1954, pp. 32–34) from the Hamilton (Arkona) Shale of Ontario, but differs from both species in a somewhat narrower dorsal cup, slightly longer brachials, and trapezoidal outline of right posterior radial. It is also distinguished from *D. crassidactylus* Laudon (1936, p. 64) from the Cedar Valley Formation of Iowa in being smaller, and in a narrower dorsal cup and longer brachials; from *D. rugistriatus* Goldring (1923, pp. 432–4) from the Portage (Ithaca) Beds of New York in lacking striations on the arms and in shorter brachials; from *D. nereus* (Hall) (Goldring 1923, pp. 419–20) from the Hamilton (Moscow) Shales of New York in having shorter primaxils, and shorter secundibrachs. From Germany, *Denariocrinus ferula* W. E. Schmidt 1941 differs in being larger, in having four anal plates in the cup, and in bearing pinnules on each secundibrach. *Rhadinocrinus minae* (W. E. Schmidt 1905) (listed as *Denariocrinus minae* by Spriestersbach 1942), from the upper Middle Devonian in Germany, is similar in size and shape, but differs fundamentally in having three primibrachs in each arm, and a radianal that is smaller than anal X, a feature of the Botryocrinidae.

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THE BRACHIOPOD GENUS *VALDIVIATHYRIS* HELMCKE

by A. J. ROWELL

ABSTRACT. The type species of *Valdiviathyris* Helmcke 1940, which is known only from one specimen, is considered to be a young craniaceid, closely related to, if not actually congeneric with, *Ancistrocrania* Dall. The family Valdiviathyridae Helmcke is regarded as a junior synonym of Craniidae Forbes.

DURING the course of a revision of the inarticulate brachiopod genera for the forthcoming volume H of the *Treatise on Invertebrate Paleontology* it was necessary to examine the Recent genus *Valdiviathyris* Helmcke. The type species, *V. quenstedti* Helmcke, is known only from one specimen of the dorsal valve of the type species (Helmcke 1940, p. 222). This was obtained by the Deutschen Tiefsee Expedition in 1899 from their station 165, 38° 40' 00" S., 77° 38' 06" E., near the island of St. Paul in the southern Indian Ocean, at a depth of 672 m.

The specimen (Pl. 68, figs. 1, 5–7) was described in detail by Helmcke (1940, pp. 237–9). It is irregularly conical in form with sub-central apex, externally smooth except for growth lines and is rather small (length 2.5 mm., width 4.7 mm., height 1.3 mm.). It is characterized by having a thin, calcareous, punctate shell. The punctae originate on the inner side of the shell as simple tubes, but rapidly split up into four or five branches. Internally there are a pair of 'crura' which arise near the apex and project into the valve. Two pairs of muscle scars are visible, an anterior pair, lateral and slightly

EXPLANATION OF PLATE 68

The specimens in figures 3–7 were coated with ammonium chloride before photographing. Repositories: *Ancistrocrania parisiensis* Nos. B. 34, 482 and B. 34, 483, Sedgwick Museum, Cambridge. *Valdiviathyris quenstedti*, Brachiopod Catalogue No. 198, Institut für Spezielle Zoologie, Humboldt Universität zu Berlin. *Crania anomala*, Author's Collection, Department of Geology, University of Nottingham.

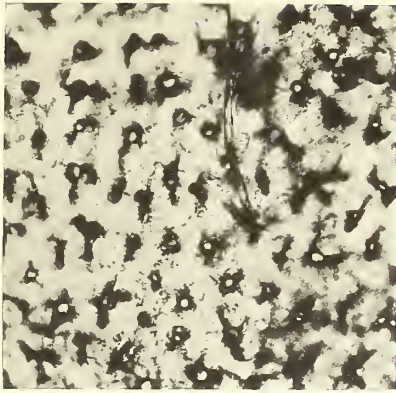
Fig. 1. *Valdiviathyris quenstedti* Helmcke. Part of the dorsal valve viewed from the inside in transmitted light, stellate appearance of the punctae due to branching. $\times 100$. Specimen No. 198. Recent. Station 165, Deutschen Tiefsee Expedition 1899 near St. Paul, South Indian Ocean, depth 672 m.

Fig. 2. *Crania anomala* (Müller). Transverse section of part of a dorsal valve viewed in transmitted light, showing punctae branching arborescently at their distal ends. $\times 150$. Recent. South-east of Garbh Reisa, coast of Argyll, W. Scotland.

Figs. 3–4. *Ancistrocrania parisiensis* (Defrance). 3, Dorsal exterior. $\times 2$. B. 34, 482. Lunata zone, U. Cretaceous; Trimmingham, Norfolk. 4, Dorsal interior showing muscle scars, postero-ventrally directed processes, small median septum and submarginal papillose flange. $\times 2$. B. 34, 483. Lunata zone, U. Cretaceous; Trimmingham, Norfolk.

Figs. 5–7. *Valdiviathyris quenstedti* Helmcke. Specimen No. 198. 5, Dorsal exterior, lateral view. $\times 6$. 6, Dorsal exterior, $\times 6$. 7, Dorsal interior showing muscle scars, dorsal processes, punctae and submarginal papillose flange. $\times 12$.

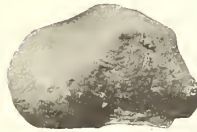
Fig. 8. *Palaeocaris* cf. *retractata* Calman, left lateral view of specimen, BU 733, $\times 9$. Coated with ammonium chloride.



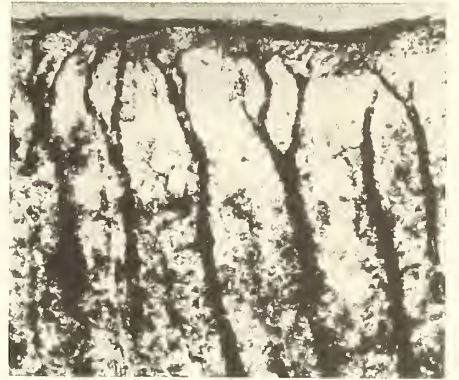
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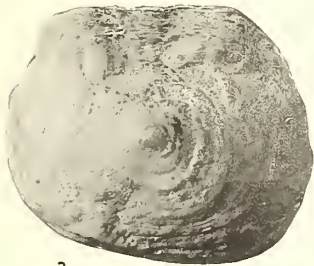
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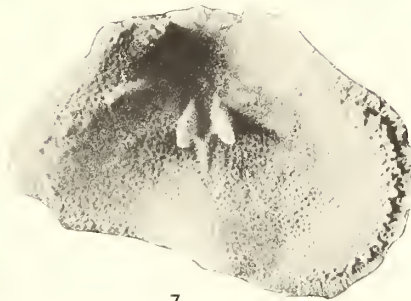
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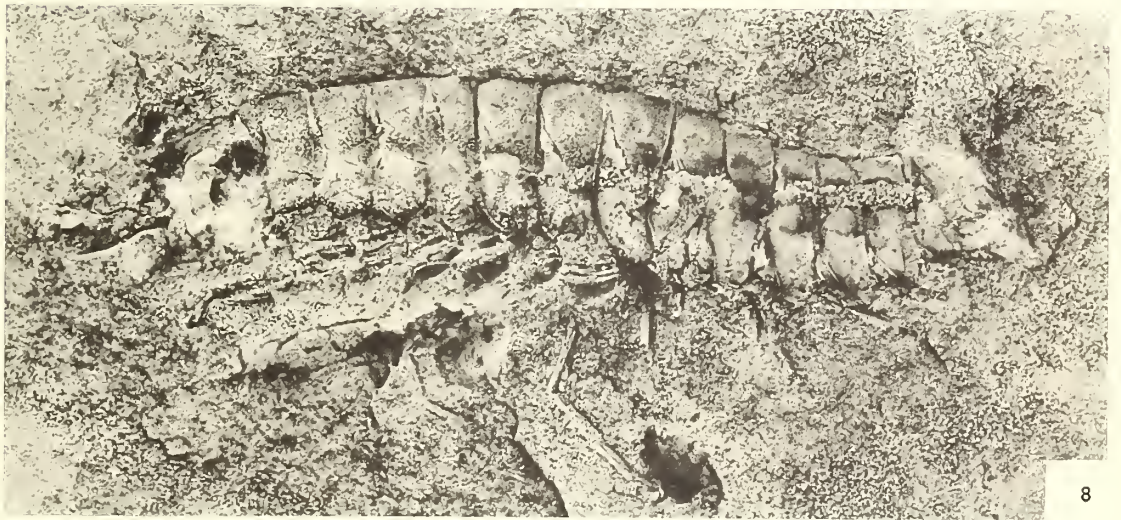
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7



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8

behind the 'crura', and a posterior pair, less distinctly marked, near the posterior margin. Helmcke did not describe this latter pair of muscles, but this is a relatively minor disagreement. The interpretation of indifferently preserved scars in inarticulate brachiopods is particularly subjective. Except for this difference, I agree completely with Helmcke's description of the specimen.

Helmcke realized that the gross morphology of the shell, its composition and irregular holoperipheral growth suggested the Craniidae, but in his opinion there were two major difficulties in putting the genus in this family. First, the nature of the punctae which are unlike those in the dorsal valve of any described adult craniaceid, and second the presence of the 'crura' which he thought were comparable to those of the terebratulaceid genus *Kraussina* Davidson. He considered that it was unlikely that there was any close relationship between *Valdiviathyris* and the Craniidae and consequently erected a new family Valdiviathyridae for the one genus *Valdiviathyris* stating that 'Da der Weichkörper dieser Tiere unbekannt ist, erscheint es nach diesen wenigen Merkmalen der Hartteile angebracht, diese neue Familie zwischen die beiden Familien der Craniidae und Terebratulidae einzureihen' (Helmcke 1940, p. 235).

The latter statement, if correct, is of considerable importance. No fossil genus of the Inarticulata hitherto examined shows characters in any way transitional between the Inarticulata and the Articulata. Indeed the fossil evidence clearly suggests that the two major divisions of the brachiopoda have been distinct from each other since the beginning of the Cambrian. Yet in Helmcke's view, we have in the Recent family Valdiviathyridae a group morphologically transitional between them. It is this surprising systematic position of the family, between the Craniidae and Terebratulidae, which makes a re-investigation of the genus very desirable.

Having essentially accepted Helmcke's description of the specimen, one can only challenge his interpretation of the structures and his views on the taxonomic position of the animal. Muir Wood (1955, pp. 63-64) has already indicated her doubts about the latter point and has tentatively included the family in the Craniacea, a conclusion with which I agree. It is possible now to substantiate this point of view and suggest a more restricted relationship of *Valdiviathyris* within the Craniacea. It would appear that Helmcke has over-emphasized the difficulties of assigning *Valdiviathyris* to the Craniidae and that both the nature of the punctae and the presence of 'crura' can be reconciled to a systematic position within this family.

The punctae of *Valdiviathyris* with their short simple tubes rapidly splitting into several branches, admittedly do not closely resemble the punctae of adult *Crania*. They are, however, basically similar to the outer, arborescently branching part (Pl. 68, fig. 2) and with the punctae in young stages of *Crania anomala* (Müller) (Rowell 1960, p. 40). The outer branching part of the puncta of adult *Crania* is formed early in the secretion of that particular part of the shell, before the fine thread-like papillae have united to form a single papilla projecting from the mantle. The inner part of the puncta, the simple tube showing only occasional branches, is formed later as the shell is thickened. In adult *C. anomala* this outer part of the punctae varies in length, but is usually between 0.06 and 0.12 mm. This is comparable with the shell thickness in *Valdiviathyris*, but it is difficult to measure this in the specimen of *V. quenstedti* without risk of damaging it. The shell is, of course, thickest at the apex and tapers to nothing at the margin of the valve, but the mean thickness is in the order of 0.1 mm. So the punctae in *Valdiviathyris*

are comparable in size as well as in structure with the arborescent part of the punctae of *Crania*. It appears then that the punctae of *Valdiviathyris* are of craniaceid type and that they differ from those of a typical adult *Crania* simply because the shell has not been thickened. It is here suggested that the specimen of *V. quenstedti* is a juvenile craniid, although the possibility that it is an adult of a very thin shelled stock cannot be eliminated. Such thin shells are very rare amongst the post Palaeozoic Craniidae.

Helmcke's second difficulty was the presence of the two ventrally directed processes in the dorsal valve, the structures which he considered to be 'crura' (Pl. 68, fig. 7) associated with the support of the lophophore. There is no direct evidence to suggest that these structures ever had such a function. Moreover, somewhat similar fulcra are already known in the dorsal valves of some Craniacea. Dall (1871, p. 72) describes the 'two slender pointed apophyses divaricating from the internal apex of the upper valve', which are typical of the craniid *Ancistrocrania* Dall, type species *A. parisiensis* (Defrance) (Pl. 68, Figs. 3-4). Similar processes occur in the dorsal valves of the related Recent species *A. japonica* (Adams) and *A. skeatsi* Allan, although as Allan (1940, p. 279) has pointed out, these two species may not be congeneric with *A. parisiensis*. There is no doubt, however, that these three species are all members of the Craniidae. In the adult *Ancistrocrania* the two processes are directed postero-ventrally (Pl. 68, fig. 4), a direction which suggests that it is very unlikely that they supported the lophophore. In the adult condition they may have been in part associated with the seat of attachment of the anterior adductor muscles. In view of the other characters of the shell of *Valdiviathyris* it seems inherently more probable that the dorsal processes in this genus are comparable with the early stages in the development of the processes in *Ancistrocrania*, rather than with a loop of terebratulaceid type.

Unfortunately, the young stages of *A. parisiensis* are unknown and it is impossible to compare *V. quenstedti* with specimens of *A. parisiensis* in a similar stage of development or size. Consequently, it is difficult to know what taxonomic weight should be given to the differences in the dorsal processes in these two species and the presence of a small triangular septum in *A. parisiensis*. In view of this uncertainty it is preferable to retain *Valdiviathyris* as a distinct genus rather than place it in synonymy with *Ancistrocrania*, but at the same time recognizing the possibility that the discovery of more material may well show them to be congeneric.

It is considered that *Valdiviathyris* is a craniaceid, and as it is not felt desirable at present to have a separate family for craniaceids possessing ventrally directed processes in their dorsal valves, the family *Valdiviathyridae* Helmcke 1940 is here regarded as a junior synonym of *Craniidae* Forbes 1838.

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A SYNCARID CRUSTACEAN FROM THE KEELE BEDS (STEPHANIAN) OF WARWICKSHIRE

by W. D. IAN ROLFE

ABSTRACT. A specimen of *Palaeocaris* cf. *retractata* Calman 1932, collected by Dr. F. Raw from the Upper Carboniferous Keele Beds of the Lickey Hills, Birmingham, is briefly described. This occurrence of the genus (which is best represented in non-marine deposits of Westphalian age) is the youngest known, and enlarges the meagre fauna recorded from the Keele Beds.

DR. F. RAW'S find of a rare syncarid crustacean is a welcome addition to the meagre fauna known from the Keele redbeds. The single specimen was collected between 1920 and 1925, from a red 'millet-seed' ironstone in the Keele Beds, on the west flank of Bilberry Hill in the Lickey Hills, south-west of Birmingham (at long. 2° 00' 13" W., lat. 52° 22' 37" N.). Dr. Raw's own notes show that the specimen was found 'in an excavation in the pathway bordering the hill, adjoining the quarry in the Cambrian quartzite'. On the sketch-map of this region given in Garrett, Hardie, Lawson, and Shotton (1958, fig. 3, p. 15) the locality is situated at a point 9 millimetres due north-east of Lickey church. Dr. Raw had correctly identified the crustacean as 'probably one of the Anaspidacea'. The specimen, BU 733, is deposited in the geology department museum, Birmingham University. Abbreviations in parentheses refer to symbols on text-fig. 1.

Subclass MALACOSTRACA Latreille 1806
Superorder EUMALACOSTRACA Grobben 1892
Order SYNCARIDA Packard 1885
Suborder ANASPIDACEA Calman 1904
Family PALAEOCARIDIDAE Siewing 1955
(*nom. correct.* herein *ex* Palaeocaridae Siewing 1955)
Genus PALAEOCARIS Meek and Worthen 1865
Type species: *P. typus* Meek and Worthen 1865
Palaeocaris cf. *retractata* Calman 1932

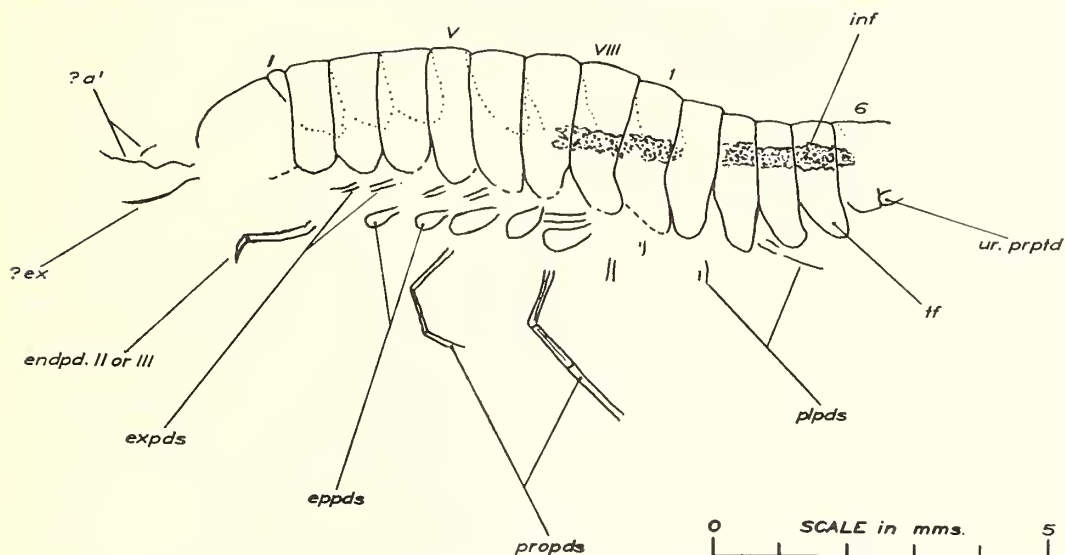
Plate 68, fig. 8; text-fig. 1

Body. The specimen is preserved in low relief, but has been crushed obliquely on to its left side, making the body appear unusually deep. Details of the head and anterior limbs are not preserved and the end of the sixth abdominal segment and the telson are missing.

The length from the front of the head to the broken-off end of the sixth abdominal segment is 11.8 mm. The head is 1.3 mm. long, but has been crushed and filled with ?kaolinite obscuring any morphological detail. The thorax is 6.0 mm. long and comprises eight smooth segments. As may be seen from Pl. 68, fig. 8, and text-fig. 1, the small first segment (I) wedges out ventrally only 0.7 mm. below the dorsal border of the head. The fifth thoracic segment (V) is noticeably shorter (0.70 mm.) than the other thoracic segments (0.75–0.90 mm.). Tergal folds are present on all segments except the

last abdominal (6), but they are better developed on the posterior thoracic and abdominal segments. The abdomen is 4.5 mm. long and composed of five smooth segments *c.* 0.6 mm. long and a longer sixth, pre-telson segment (6) of which 1.1 mm. is preserved.

Appendages. Traces of two segmented flagella and a flattened structure in front of the head are doubtfully suggested from their position to be an antennule (*a*¹) and the exopodite (or scale) of an antenna (?*ex*). No other cephalic appendages are visible.



TEXT-FIG. 1. Outline drawing of *Palaeocaris cf. retractata* Calman, BU 733. ?*a*¹, antennule; ?*ex*, exopodite of antenna; eppds, possibly pereopod epipodites; endpd II or III, endopodite of second or third pereopod; propds, propodites of pereopod endopodites; expds, traces of pereopod exopodites; plpds, traces of pleopods; tf, tergal fold; ur. prptd, protopodite of uropod; inf, intestine infilling; I–VIII, thoracic segments; 1–6, abdominal segments; dotted lines indicate impressions of tergal folds on other side of body.

The endopodite of the second or third pereopod (endpd II or III) has fortunately been preserved and is seen to be no stouter than the endopodites of the other thoracic limbs. The 'knee' or main flexure of the thoracic endopodites is only preserved in two limbs. Following Calman (1932, p. 539), the segment proximal to the knee is taken as the meropodite and hence the two distal segments discernible are the carpopodite and the propodite (propd). Traces of the exopodites of the pereopods are present but no details of segmentation can be discerned. Immediately ventrad of the last five thoracic segments and exopodites are five concave, oval structures (eppds), which may represent epipodites (see discussion below). Only traces of pleopods are discernible. The pre-telson segment (6) bears a fragment of the protopodite of one uropod (ur. prptd).

An interrupted band of millet-seed siltstone particles marks the original course of the intestine (*inf.*).

Comparison with known forms. R. Siewing has recently listed most of the known fossil syncarids, but the following emendations are necessary to his 1959 account (pp. 100–3).

Synonymies of the genus *Uronectes* Bronn 1850 have been given by Cockerell (1916, p. 235), Haack (1927, pp. 773–4), van Straelen (1931, p. 18) and Calman (1934, p. 323). Siewing (p. 1) figures Fritsch's 1901 'restoration' of this genus but fails to take account of Calman's criticisms (1934, p. 321). Thus, there is no seventh abdominal segment (Haack 1927, pp. 775, 785; Calman 1934, p. 325, and cf. Tiegs and Manton 1958, p. 294). A specimen of *U. fimbriatus* (Jordan), in the Museum of Comparative Zoology, Harvard College (MCZ 6061), shows dorso-ventral wrinkling of the long sixth abdominal segment, probably caused by impaction of the telson. Fritsch's taf. 158, fig. 2, shows what is clearly a crack or fold in the last abdominal segment in the same position as the spurious boundary between the sixth and seventh abdominal segments on taf. 159 and fig. 377 (1901). Thus there is no evidence for a distinct Order Gampsonychidea Packard 1886 (cf. also Siewing 1955, p. 241; 1956, pp. 155, 159) based primarily on the presence of an extra abdominal segment. The genus *Uronectes* and the family *Uronectidae* Cockerell 1916 should be replaced in the suborder Anaspidae Calman 1904, as shown by Calman (1934, pp. 322–3).

Palaeocaris scotica Peach 1881 was made the type of a new genus *Anthracocaris* of the ?Tanaidacea by Calman in 1933, and it and *P. landsboroughi* Peach 1908 should be removed from the Syncarida (cf. Siewing, p. 101).

The present specimen can be excluded from the genera *Uronectes* and *Acanthotelson* Meek and Worthen 1865, on the basis of the following characters:

A short fifth thoracic segment such as is present in this specimen is characteristic of both *Palaeocaris* and *Uronectes* (Calman 1911*b*, p. 490; 1934, p. 325; Haack 1927, p. 776) but not *Acanthotelson* (Meek and Worthen 1865, p. 48; 1866, p. 403). Further, *Acanthotelson* lacks thoracic tergal folds (Calman 1911*a*, p. 159), and has its sixth abdominal segment equal in length to the preceding segments (Meek and Worthen 1865, p. 48; 1866, p. 403, pl. 32, fig. 6; 1868, p. 549, figs. A, B; Calman 1911*a*, p. 159), whereas in both *Palaeocaris* and *Uronectes* this segment is always longer (Calman 1934, p. 325). The presence of an unmodified second or third thoracic pereopod is significant, since *Uronectes* can only be distinguished from *Palaeocaris* 'by the enlargement of the second and third pairs of thoracic limbs' to form large raptorial appendages (Calman 1934, p. 329).

The genus *Triasocaris* Bill 1914 is distinguished by its large rostrum, and *Pleurocaris* Calman 1911 by its large thoracic tergal folds and transverse striation of the body segments. *Nectotelson* Brocchi 1880 is too poorly preserved to be distinguished from *Palaeocaris* or *Uronectes* (cf. Calman 1934, p. 323), and *Palaeorchestia* Zittel 1882 and *Belotelson* Packard 1886 are probably synonyms of *Palaeocaris*. The affinities of *Gasocaris* Fritsch 1901, from the Upper Westphalian of Czechoslovakia, are unknown.

The specimen most closely resembles *Palaeocaris retractata* Calman 1932. *P. vandergrachti* Pruvost, from the Namurian of Belgium, is very similar and agrees with the present specimen in showing an identically reduced first thoracic segment when compared with *P. praecursor* (Woodward), as figured by Calman (1911*b*, fig. 2A). Pruvost (1930, p. 182) suggested that this reduction was due to displacement of the first thoracic segment behind the second, but such unduly shallow first segments could also be explained by oblique instead of truly lateral flattening exposing more of the sternal region and less of the tergite. The lack of a counterpart to the present specimen prevents any certainty on this point, but the vertical displacement of the tergal folds on opposite

sides of the body, shown dotted on text-fig. 1, indicates that the specimen was flattened obliquely. The degree of incorporation of the first thoracic segment with the head is an important character in syncarid classification and phylogeny, as Calman has amply shown (1917, pp. 502–11). Should other syncarids be found possessing genuinely reduced first thoracic segments which can be shown to be not due merely to distortion, a new genus and family would be required.

In the absence of the telson and uropods the specimen cannot be distinguished from *P. lohesti* van Straelen. *P. praecursor* (Woodward) 1908 and *P. burnetti* Woodward 1881 show striae on the body segments, and *P. typus* Meek and Worthen 1865 is usually larger. These criteria are hardly sufficient for specific differentiation, however, and the three latter species are possibly synonymous (Calman 1911*b*, p. 492).

The five oval structures of the present specimen referred to as epipodites are identical with the four 'oblong depressed areas' at the bases of the last four thoracic limbs of *Palaeocaris praecursor*, described and figured by Calman (1932, fig. 2, p. 539). Although Calman was tempted to interpret these as branchial epipodites like those of modern *Anaspides* he was 'not inclined to attach much weight to it' in view of their fragility in the modern form (1932, p. 539). In 1934 he rejected this interpretation and suggested that they were 'only the side-plates (pleura [=tergal folds]) of the opposite side exposed owing to the somewhat oblique compression of the body' (p. 328). Although one must certainly agree with Calman's reservations, it still seems better to interpret these structures as epipodites. In the present specimen they are certainly not tergal folds of the opposite side and neither exopodites nor endopodites show such concave, oval structures. Epipodites (and exopodites) are wanting on the last thoracic limb of *Anaspides* and only reduced epipodites are present on the seventh pair (Calman 1896, p. 792). If the above interpretation is correct the fossil forms are noteworthy in possessing epipodites as well as exopodites (Calman 1932, p. 539) on this last thoracic segment.

P. ?cuylerensis Wells 1957 and *P. destinezi* van Straelen 1943 are Middle and Upper Devonian marine species. *P. novascotica* Copeland 1957, from the Lower Carboniferous of Canada, has only six thoracic segments (Copeland 1957, p. 596 and also kindly confirmed in a personal communication from Dr. Copeland) and thus is not a syncarid. It possibly belongs to Calman's genus *Anthracocaris*.

Occurrence. *P. ?cuylerensis*, *P. destinezi*, *P. lohesti*, *P. vandergrachti*, and *Clarkecaris brasiliica* (Clarke) are the only syncarids known from supposedly marine beds; they are of Middle and Upper Devonian, Namurian, Lower Westphalian, and ?Lower Permian ages respectively. The known English syncarids and the majority of non-English syncarids are of Westphalian age, and are generally found in coal-measure ironstone concretions. The specimens of *P. praecursor* from Shipley Hall estate, Derbyshire, quoted by Calman (1932, p. 537) as 'Ouralian' [=Stephanian], were collected from below the Top Hard [=Barnsley] Coal (Moysey 1911, p. 506) and hence are of Westphalian age (see Stubblefield and Trotter 1957, pl. 1). *P. retractata* is known only from the Westphalian of Coseley, near Birmingham. Specimens were collected from 'binds between the Brooch and Thick coals' (Bolton 1921, p. 20), which is a little higher in the Middle Coal Measures than the Shipley locality.

The post-Westphalian fossil syncarids are *Nectotelson* [?= *Palaeocaris*] *rochei* Brocchi, from the 'Autunian' (Lower Permian) of France, *Uronectes fimbriatus* (Jordan), and

Clarkecaris brasiliica (Clarke), from the Lower Permian of Saarland and Brazil, and *Triasocaris peachi* Bill, from the Triassic Bunter sandstone of Alsace. *Anaspides* (?) *antiquus* Chilton 1929, from the Triassic Hawkesbury Sandstones of New South Wales, is presumably to be included in one of the foregoing genera.

The Keele redbeds are almost certainly of primary origin (Trotter 1953, p. 18), and their conditions of deposition have been fully discussed by Wills (1948, pp. 56–64). We may perhaps imagine the present specimen inhabiting a temporary fresh-water pool in the south of the Keele redbed playa portrayed by Wills (1956, fig. 10, p. 77). Professor Wills's record of arthropod trails from the Keele Beds (1948, p. 63) is relevant to the present discussion, and an unpublished photograph by Dr. Raw (No. 174 in the Birmingham collection) shows a trail of the type of *Ichnispica* Linck 1945, with the paired tracks 6–13 mm. apart. The smaller trails could conceivably have been left by a crustacean of the size of the present specimen.

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ADDENDUM

While this paper was in press, A. Vandenberghé's paper appeared (1961, *Bull. Soc. géol. Fr.* 2, 5, 690–2) demonstrating the syncarid nature of the previously doubtful genus *Eileticus*. *Eileticus* is a member of the family Pleurocarididae Chappuis 1915 [= Acanthotelsonidae Pruvost 1919; Eileticidae Vandenberghé 1961] which is distinguished from the Palaeocarididae by having the first thoracic segment incorporated with the head. The two subfamilies proposed by Vandenberghé require changes, thus: Pleurocaridinae [*nom. transl. et correct.* herein (*ex* Pleurocarididae Chappuis 1915)] [= Acanthotelsonidae Vandenberghé 1961]; Eileticinae [*nom. transl.* herein (*ex* Eileticidae Vandenberghé 1961)] [= Anacanthotelsonidae Vandenberghé 1961 (*nom. nud.*)]. Vandenberghé states that *Eileticus* has a seventh abdominal segment, although by analogy with *Uronectes* this appearance may solely be due to the extra length of the sixth segment. In either case this would provide a further distinction from the Pleurocaridinae; the nature of the head, together with the absence of limbs from the described specimens, prevents closer comparison with the Uronectidae.

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UPPER CRETACEOUS PLANKTONIC FORAMINIFERA FROM THE ISLE OF WIGHT, ENGLAND

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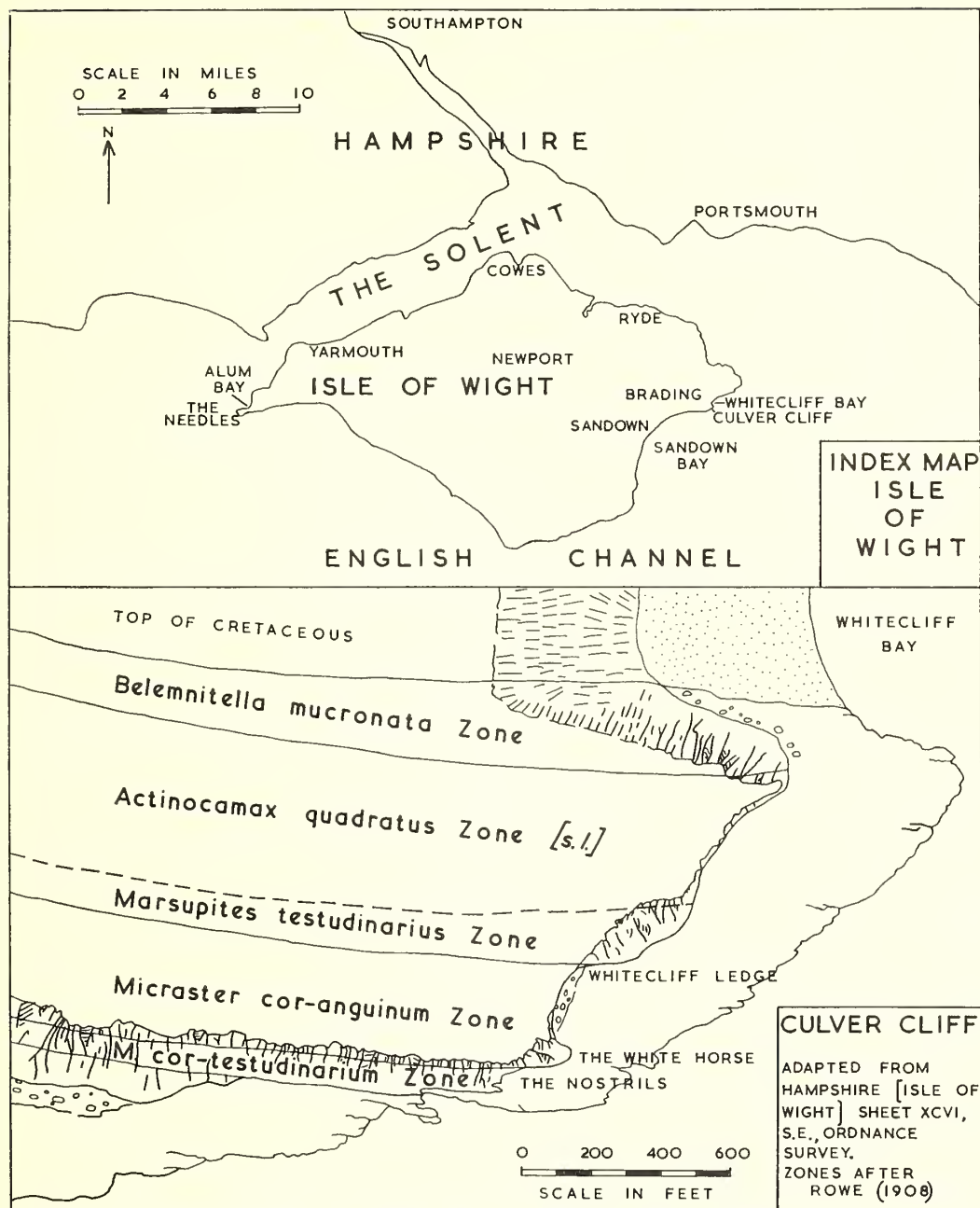
ABSTRACT. Seventeen species and subspecies of planktonic Foraminifera are recorded from approximately 1,000 feet of Senonian Upper Chalk from Culver Cliff, Isle of Wight. Four species, *Planomalina ehrenbergi*, *P. rowei*, *Schackoina cushmani*, and *Globotruncana culverensis*, are described as new. Planktonic-benthonic ratios suggest a neritic or upper bathyal environment for the deposition of most of the Upper Chalk. There is indication of a shallowing of the Upper Cretaceous sea at the beginning of the *Belemnitella mucronata* Zone.

MUCH emphasis has been placed on the study of planktonic Foraminifera during the last 15 to 20 years. The short stratigraphical ranges and wide geographical distribution of many planktonic Foraminifera make them exceptionally useful in correlating strata of diverse facies and over great distances. Planktonic Foraminifera have been studied in great detail from Upper Cretaceous rocks of the Caribbean area (Bolli 1951, 1957, 1959; Brönnimann 1952; Gandolfi 1955), Northern Africa (Dalbiez 1955; Sigal 1949, 1952), and continental Europe (Bolli 1945; Cita 1948; Reichel 1950; Hofker 1956), to mention only a few areas. However, there is little mention in the literature of the planktonic Foraminifera from the extensive Cretaceous rocks of the British Isles.

The purpose of this paper is to describe the planktonic Foraminifera from the Upper Chalk (Senonian) at Culver Cliff, Isle of Wight, and to record their stratigraphical ranges. It is hoped that this and forthcoming studies of the Upper Cretaceous Foraminifera will aid in the more precise dating and correlation of the British Chalk.

Location. Over 1,200 feet (Rowe 1908, p. 285) of steeply dipping Upper Cretaceous chalk are well exposed at Culver Cliff, the sea cliffs just south of Whitecliff Bay, on the east-central coast of the Isle of Wight. The impressive exposures of Culver Cliff are located about 2½ miles north-east of Sandown and approximately 2 miles south-east of Brading. The base of the sea cliffs from the *Belemnitella mucronata* Zone to the Upper *Micraster cor-testudinarium* Zone can best be reached from Whitecliff Bay, whereas the basal beds of the *M. cor-testudinarium* Zone and underlying strata must be approached from Sandown Bay to the south. The base of most of the sea cliffs can only be reached during periods of low tide.

Procedure. Most of the Upper Chalk (Senonian) was measured by means of a tape and Brunton compass traverse. Samples for foraminiferal analysis were collected along the traverse. Traverse data were reduced to stratigraphic thickness through use of Mandelbaum and Sanford's (1952) tables. Chalk, marly chalk, and chalk meal from the insides of cavernous flint nodules were processed for foraminiferal analysis. The chalk meal from the flint nodules contained, by far, the most abundant and best-preserved Foraminifera. Samples were disaggregated by heating in a dilute solution of hydrogen peroxide for several hours. Residues were then washed through a 120-mesh sieve (average opening



TEXT-FIG. 1. Location map of Culver Cliff, Isle of Wight.

124 microns); also, finer residues were frequently examined. The Foraminifera were concentrated by floating processes using carbon tetrachloride. The remaining residues were also examined for species less susceptible to concentration by floating methods.

Planktonic-benthonic ratio calculations were made from counts of all Foraminifera in representative portions of each sample before concentration by floating. These representative samples were obtained by splitting the washed residues with a micro-sample splitter, described by Kennard and Smith (in press), to a size containing 300 to 500 Foraminifera.

Deposition of types. Holotypes and illustrated specimens are deposited in the British Museum (Natural History), London. Paratypes and additional material are deposited in the collections of University College, University of London.

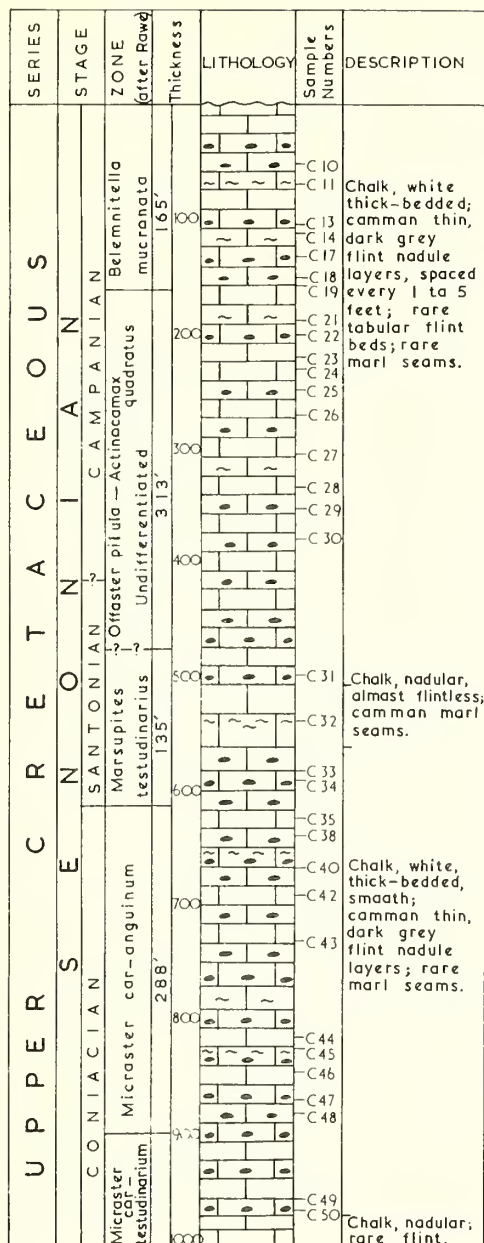
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STRATIGRAPHY

In the first half of the nineteenth century geologists began subdividing the Upper Cretaceous chalk of the British Isles into local lithological units or formations. These units were later grouped into the larger units, Upper, Middle, and Lower Chalk, which could generally be recognized over large areas. It soon became apparent that these lithological units had distinctive fossil assemblages. The terms Upper, Middle, and Lower Chalk were then applied to units entirely defined by fossil content, thus having time-stratigraphic significance, but were approximate equivalents to the older lithologic units.

In 1875 the French geologist Barrois made the first serious attempt to zone the Chalk on the Isle of Wight. The next year Barrois (1876) completed a stratigraphic study of the Upper Cretaceous rocks of England and Ireland and showed that it was possible to use the same megafossil zones in the British Isles as were established in the Upper Cretaceous of France, and these zones could be grouped into the stages proposed by d'Orbigny. The zones used by Barrois (1876) are as follows:

STAGES	ZONES
Senonian	{ Zone of <i>Belemnites</i> Zone of <i>Marsupites</i> Zone of <i>Micraster cor-anguinum</i> Zone of <i>Micraster cor-testudinarium</i>



TEXT-FIG. 2. Columnar section of Upper Chalk at Culver Cliff showing stratigraphic position of samples.

Turonian	{	Zone of <i>Holaster planus</i>
	{	Zone of <i>Terebratulina gracilis</i>
	{	Zone of <i>Inoceramus labiatus</i>
Cenomanian	{	Zone of <i>Belemnites plenus</i>
	{	Zone of <i>Holaster subglobosus</i>
	{	Chloritic Marl
	{	Zone of <i>Pecten asper</i>
	{	Zone of <i>Ammonites inflatus</i>

The Zones of *Pecten asper* and *Ammonites inflatus* are now placed in the Albian Stage. The Senonian and Turonian stages of d'Orbigny are approximately equivalent to the Upper and Middle Chalk, respectively. The *Holaster planus* Zone, however, is placed in the Upper Chalk (see Jukes-Browne (1903, pp. 1–10) for a more complete discussion of the early stratigraphic nomenclature of the Upper Cretaceous of Great Britain).

Rowe (1908) published the results of an extensive study of the Chalk of the Isle of Wight, and for the first time clearly defined the zonal divisions of the Upper and Middle Chalk in this area and mapped their boundaries throughout much of the island. He subdivided the Upper Chalk of the Isle of Wight into the following zones:

Zone of *Belemnitella mucronata*
 Zone of *Actinocamax quadratus*
 Zone of *Marsupites testudinarius*
 Zone of *Micraster cor-anguinum*
 Zone of *Micraster cor-testudinarium*
 Zone of *Holaster planus*

In 1912 Brydone subdivided the Zone of *Actinocamax quadratus* in Hampshire, Sussex, and Wiltshire into two zones, retaining the name *A. quadratus* for the upper zone and proposing the name *Offaster pilula* for the lower zone. In the same year Jukes-Browne (1912) also subdivided the Zone of *A. quadratus* into two zones and proposed the name '*Offaster pilula*' for his lower zone. Later, Brydone (1914, p. 404) extended his study to the Isle of Wight and recognized the Zones of *O. pilula* and the restricted *A. quadratus* at Scratchells Bay on the western shore; however, because of the poor condition of the exposures, he was not able to subdivide the unrestricted Zone of *A. quadratus* at Culver Cliff.

Micraster cor-testudinarium Zone. This zone is exposed at the base of the south-easternmost portion of Culver Cliff which may be approached only during periods of exceptionally low tides. Because of the inaccessibility of the basal beds, only the uppermost 90 feet of this zone were examined. According to Rowe (1908, p. 242), the top of the *M. cor-testudinarium* Zone 'may be placed at the point where the out-jutting cliff called White Horse joins the surface in which the northern Nostril is cut'. The lowermost 15 feet of the examined beds consisted of very hard, often nodular, thick bedded, aphanitic white chalk containing very little flint. The uppermost 75 feet of this unit contain common flint nodule layers, spaced every 1 to 3 feet, which probably represent the highest percentage of flint found in the Upper Chalk at Culver Cliff. The flint is dark brownish-grey to black and the nodules vary greatly in size and shape, usually

ranging from 1 to 10 inches in length. Marl seams are rare; and in the upper part of this zone there are several chalk layers containing numerous *Inocerami* fragments.

Micraster cor-anguinum Zone. The *M. cor-anguinum* Zone is exposed at Culver Cliff between the northern Nostril and the southern base of the east-west trending Whitecliff. In the central portion of this unit a large slide of chalk obscures the base of the cliff. This zone has a thickness of 288 feet and consists of a thick bedded, very pure, aphanitic, white chalk which contains very rare glauconite and subangular quartz grains. Most of the chalk has a smooth appearance; however, some nodular chalk bands are present near the base of the zone. There are several beds of chalk containing abundant *Inocerami* fragments in the basal 30 feet. Brownish-grey to black flint nodule layers, similar to those of the *M. cor-testudinarium* Zone, are common throughout the zone, occurring every 1 to 3 feet. These flint nodules are rarely cavernous; however, on the north and south walls of White Horse are several very thin layers containing small, nearly spherical, flint nodules about $\frac{1}{2}$ to $1\frac{1}{2}$ inches in diameter which are often hollow and usually contain very fossiliferous chalk meal.

Marsupites testudinarius Zone. As early as 1865 Whitaker (p. 404) mentioned the presence of a unit of nearly flintless chalk at Culver Cliff and his often-quoted words are as follows: 'Here in the midst of the chalk, with layers of flint at every 3 or 4 feet, is a space some 40 to 50 feet thick with only one seam of tabular flint, but with four lines of green coated nodules like those of the Chalk Rock, but perhaps of a deeper colour.' Rowe (1908, p. 245) described a nearly flintless section of strata about 58 feet thick containing 4 nodule beds and put the contact of the *M. testudinarius*-*Actinocamax quadratus* Zones between the 2 lowest nodule beds, thus placing about 12 feet of the flintless unit in the *M. testudinarius* Zone and the bulk of the unit in the *A. quadratus* Zone. Rowe (op. cit., pls. 19, 20, F) has very clearly plotted this unit on excellent photographs of Culver Cliff; and on the map accompanying his work, Sherborn has plotted this same zonal boundary. However, the present author has observed the very distinctive, nearly flintless unit about 55 feet in thickness with the greenish chalk nodule layers and 2 tabular flint beds located entirely within the *Marsupites testudinarius* Zone as delimited by Rowe on his plates and on the accompanying geological map by Sherborn. In Rowe's photograph (pl. 19, p. 329) of the cliff section designated as the 'belt of flintless chalk and the nodule beds', the present author has found about 20 flint nodule beds and 3 tabular flint layers. On close inspection of Rowe's plate 19, several flint nodule beds can be seen within the 'flintless chalk' high on the cliff above the algal cover. Rowe has either: (1) misplotted the nearly flintless chalk unit; or (2) misidentified this unit.

If we assume that Rowe misidentified this unit and used the upper boundary of the *M. testudinarius* Zone as shown on his plate 19 and on the accompanying geological map, this zone is composed of three units with a total thickness of 135 feet:

Chalk, common flint nodules	30 ft.
Chalk, nearly flintless with green chalk nodule layers	55 ft.
Chalk, common flint nodules	50 ft.

On the other hand, Rowe's (1908, p. 245) description of a nearly flintless chalk unit more closely fits the true flintless chalk unit than the strata present where he has placed

this unit on his plates and map. Brydone (1914, pp. 209, 210), however, gives a very detailed description of the nearly flintless chalk, which is in close agreement with the present author's observations. Although Brydone's unit has about the same thickness as that described by Rowe, he remarks that there is a wide discrepancy between their details. If we assume that Rowe misplotted the flintless chalk and that the top of the *M. testudinarius* Zone is between the two lowest green chalk nodule layers, then the zone has a thickness of approximately 65 feet and is composed of two units:

Chalk, flintless with a single green chalk nodule layer	15 ft.
Chalk, common flint nodules	50 ft.

Rowe (p. 246) reports a thickness of 95 feet for the *M. testudinarius* Zone at Culver Cliff which is intermediate between the two preceding thicknesses calculated for the zone. It is therefore still not clear where Rowe wished to place the upper boundary of this zone. In the present report the upper limit of the zone is tentatively placed approximately 30 feet above the flintless chalk unit. The lower boundary of the *M. testudinarius* Zone was located approximately by Rowe at the base of the east-west trending cliff, just above the words 'Whitecliff Ledge' on the location map.

Actinocamax quadratus-*Offaster pilula* Zones. Brydone (1914) was not able to subdivide the older *Actinocamax quadratus* Zone (s.l.) at Culver Cliff into his *Offaster pilula* Zone and *Actinocamax quadratus* Zone (s.s.), although they are both undoubtedly present as they are in east Sussex and at Scratchell's Bay on the western side of the Isle of Wight. As has been mentioned, there is some question as to whether the base of the *A. quadratus* Zone (s.l.) should be placed within the flintless chalk or about 30 feet above this unit as it tentatively has been done in this report.

The measured thickness of the strata between the base of the *Belemnitella mucronata* Zone and the nearly flintless chalk is 345 feet, the lower 30 feet of which is placed in the *Marsupites testudinarius* Zone. Brydone (op. cit., p. 209) gives a detailed description of the strata, and reports a measurement of 355 feet for the same unit. This unit consists of thick bedded, aphanitic, white chalk with flint nodule layers spaced every 1 to 4 feet. The flint nodules are dark brownish-grey, often with light greyish tan patches in their interiors, and usually with thin white silicious coatings about $\frac{1}{8}$ to $\frac{1}{4}$ inch in thickness. The nodules in the upper part of the zone are often cavernous containing chalk meal, but are rarely cavernous in the lower beds. The greater part of the chalk meal, containing abundant coccoliths, when disaggregated will pass through a 200-mesh sieve. The coarser fraction consists chiefly of amorphous chalk, small hollow spheres about 0.06 mm. in diameter which may be inorganic or of algal origin (see Earland 1939, pp. 30-33), and Foraminifera with lesser amounts of Ostracodes, Inocerami (prisms), sponge spicules, Echinoid spines, and macrofossil fragments. Sponge spicules, although often common in the chalk meal, were not observed in the chalk. The only Radiolaria observed were rare specimens, which had been replaced by flint, from the chalk meal of the upper part of this zone and the *Belemnitella mucronata* Zone. Bryozoa are usually rare; however, about 20 per cent. of the coarse fraction of sample C-23 consists of fragments of Bryozoa. Small subangular grains of quartz, glauconite, and pyrite crystals, although very rare, were found in most of the examined samples. Marl seams are fairly common and there are about 4 tabular flint beds within this unit.

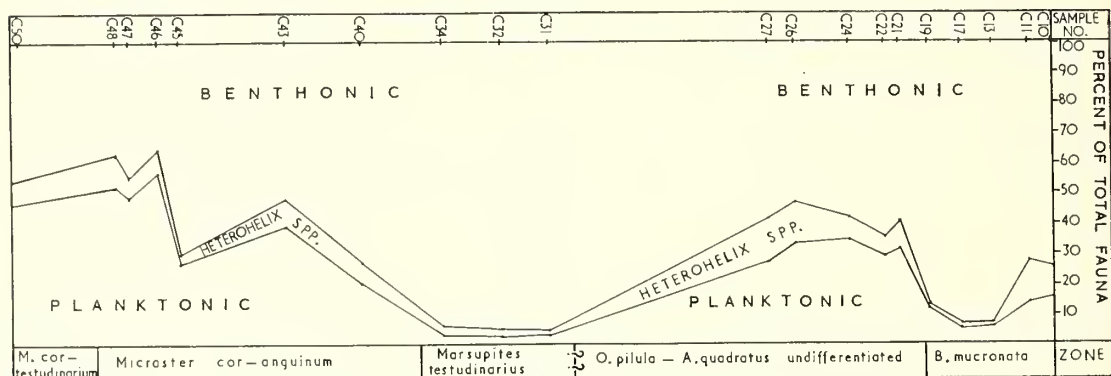
Belemnitella mucronata Zone. The *B. mucronata* Zone represents the youngest Cretaceous strata at Culver. These rocks form the prominent white cliffs of the short southern shore of Whitecliff Bay. The upper portion of this zone is largely covered at the sea cliff by chalk alluvium; however, the entire zone is exposed on the reef at low tide. These strata consist of thick bedded, white, aphanitic, very pure chalk, containing very rare glauconite, subangular quartz grains, and pyrite crystals. Although well indurated, the chalk from this zone is somewhat softer than most of the older chalk. The chalk on the reef exposed to the ocean water is noticeably harder than that high on the cliffs. Thin, dark-grey, flint nodule layers are very common, spaced every 1 to 4 feet. Many nodules are cavernous and contain very fossiliferous chalk meal similar in composition to that of the *A. quadratus* Zone. Thin marl seams, ranging in thickness from 2 to 7 inches, are fairly common especially near the base of the zone. The measured thickness of this zone across the reef is 165 feet which differs from Rowe's (1908, p. 249) reported thickness of 150 feet. The beds of the *B. mucronata* Zone are unconformably overlain by steeply dipping Lower Tertiary shales. The approximate base of this zone as located by Rowe is a ledge which runs due east near the north-easternmost part of the cliff.

ECOLOGY

Thomas Huxley, in 1858 (see Thomson, 1874), referred to the *Globigerina* ooze of the Atlantic as a 'modern Chalk'. For many years afterwards the belief was prevalent among geologists that the Cretaceous chalk deposits of Great Britain were ancient deep-sea *Globigerina* oozes. Murray and Renard (1891, p. xxviii), after their extensive study of the deep-sea deposits collected by the 'Challenger' Expedition, stated: 'The nature of the mineral action, the variability of the residue, the chemical analysis, the character of the organic remains, and the position of the Cretaceous Sea, all point to the white chalk being formed near shore, and not in the abysmal regions of a deep ocean, like a typical *Globigerina* ooze.' Even after this statement by two of the foremost students of deep-sea deposits, the idea that the chalk was a deep-sea ooze continued among some geologists for many years. Earland (1939) discussed the many lines of evidence for the depositional environment of the Chalk and concluded (p. 34): 'The Chalk was formed at the bottom of a comparatively shallow sea, whose depth varied at times between less than 50 and a maximum of about 300 fathoms.'

Jukes-Browne (1904) and others have cited the bathymetric ranges of present-day Foraminifera which they believed were also found in the Chalk as evidence for depth of deposition of the Chalk. These species have been misidentified, and very few if any Foraminifera from the Chalk have survived to the Recent. One approach that may give us information on the depth of deposition of the Chalk, however, is the ratio of planktonic to benthonic Foraminifera found in this deposit. Although Earland (1939, p. 18) states, 'For pelagic Foraminifera are by no means abundant in the chalk. Though their number varies in different zones they are always a negligible constituent and never dominant among other Foraminifera'; it was found that planktonic Foraminifera (*Globigerinaceae*) from the Upper Chalk of the Isle of Wight composed 3 to 57 per cent. of each of the examined foraminiferal assemblages, and species of *Heterohelix*, which may possibly be planktonic, make up another 1 to 13 per cent. of each foraminiferal assemblage.

Since the early studies of Recent Foraminifera it has been realized that in deep-sea deposits such as *Globigerina* ooze planktonic Foraminifera compose a much higher percentage of the foraminiferal assemblages than do the benthonic Foraminifera and that the converse is true in near shore environments. Grimsdale and Morkhoven (1955) have studied the planktonic-benthonic ratios of numerous Recent foraminiferal assemblages from the Gulf of Mexico and have shown that there is a general progressive increase in the percentage of planktonic Foraminifera with depth. This increase with depth is due largely to: (1) an increased water column which will contain a greater number of planktonic Foraminifera per square unit of ocean bottom; and (2) a general



TEXT-FIG. 3. Chart showing percentage of planktonic-benthonic Foraminifera per sample.

decrease in the number of benthonic Foraminifera with increased depth, at least, from lower neritic to abyssal depths. Phleger (1945, 1951) has shown that living planktonic Foraminifera are present in the water column down to depths of over 1,000 metres. Proximity of oceanic currents, bottom conditions, turbidity in surface waters, and numerous other ecologic factors may also locally affect the planktonic-benthonic ratios. It is obvious, therefore, that any interpretation of paleobathymetry from planktonic-benthonic ratios in Tertiary or Upper Cretaceous rocks can only be attempted in a general sense and by analysis of many samples.

The percentages of planktonic and benthonic forms from twenty foraminiferal assemblages from the Upper Chalk have been calculated. Complete counts were made of all Foraminifera present in representative portions of each sample. All assemblages but three contained 300 to 500 Foraminifera. The complete faunas were counted of samples C31, C32, and C34, each containing less than 60 Foraminifera. These three faunas which contain anomalously low percentages of planktonic Foraminifera are poorly preserved and appear to have undergone a selective destruction of certain faunal elements. It is believed that most of the fragile forms, which most often contain a high percentage of planktonics, have been destroyed by post-depositional processes; and, therefore, the ratios for these three samples may be quite unreliable. The faunas of the other seventeen samples are well preserved and there is no evidence of any selective destruction. The planktonic percentages of samples C50 to C46 from the upper *Micraster cor-testudinarium* Zone and lower *Micraster cor-anguinum* Zone range from 40 to 57

Plumage

Location & Date 1946
1947

Test ornamented by Kes.
tail and rose
features.

1. Bare in center in ph.
oblongata cap
protrusion [In the
the same as!
Glaucirella cap]

2. P. ehrenbergi
likely P. rosea cap
the same Glaucirella

LAC



per cent. Grimsdale and Morkhoven's (1955, text-fig. 1) depth distribution chart suggests 90 to 800 metres as the depth of deposition for these samples. Samples C45 to C40, from the middle and upper *M. cor-anguinum* Zone, have planktonic percentages ranging from 22 to 40 per cent. which suggest a depth of deposition of 65 to 500 metres. The percentages of planktonic Foraminifera from samples C27 to C21 from the *Actinocamax quadratus* Zone range from 28 to 35 per cent., suggesting a depth of deposition of 75 to 500 metres. Faunas from samples C19 to C10 from the *Belemnitella mucronata* Zone contain from 5 to 16 per cent. planktonics, suggesting a depth of deposition of 30 to 50 metres.

The above bathymetric ranges of deposition are very broad but agree well with Earland's estimates (1939, p. 34). The evidence from this study is not conclusive that there was any fluctuation in depositional depth from the upper *Micraster cor-testudinarium* Zone to the top of the *Actinocamax quadratus* Zone. The planktonic-benthonic ratios, however, do suggest that there was a shallowing of the Cretaceous sea in the Isle of Wight area at the beginning of deposition of the *Belemnitella mucronata* Zone. A shallowing of the Cretaceous sea at this time is in close agreement with the opinion of Jukes-Browne (1904, pp. 374-7) who came to the same conclusion from evidence along other geologic lines. The results of this study are very general indeed, and it must be kept in mind that the size of the study adds further limitations. It is hoped, however, that this may be the first step in a more encompassing study, both geographically and stratigraphically, of the percentages of planktonic Foraminifera in the Chalk of Great Britain.

SYSTEMATIC DESCRIPTIONS

Family HANTKENINIDAE Cushman 1927

Subfamily PLANOMALININAE Bolli, Loeblich, and Tappan 1957

Genus PLANOMALINA Loeblich and Tappan 1957

Planomalina aspera (Ehrenberg)

Plate 69, figs. 4a, b

Rotalia aspera Ehrenberg, 1854, p. 24, pl. 27, figs. 57-58; pl. 28, fig. 42; pl. 31, fig. 44.

Phaenostommum asperum Ehrenberg 1854, p. 23, pl. 30, figs. 26a-b.

Rotalia aspera Ehrenberg, Beissel, p. 73, pl. 14, figs. 1-6.

Globigerina aequilateralis (not Brady), Chapman 1892, p. 517, pl. 15, fig. 14.

Globigerina aequilateralis (not Brady), Heron-Allen and Earland 1910, p. 424, pl. 8, figs. 11-12.

Globigerinella aspera (Ehrenberg), Brotzen 1936, p. 170, pl. 13, fig. 2.

Globigerinella aspera (Ehrenberg), Schijfsma 1946, pp. 94-96, pl. 6, fig. 8.

Globigerinella aspera (Ehrenberg), Bandy 1951, p. 508, pl. 75, fig. 3.

Globigerinella aspera (Ehrenberg), Belford 1960, p. 91, pl. 25, figs. 4-6.

Description. Test free, planispiral with slightly trochoid initial whorl, biumbilicate, semi-evolute, loosely coiled containing 2 to 3 whorls, periphery circular, lobulate; chambers globular; 5 to 6 chambers in final whorl rapidly and uniformly increasing in size; sutures distinct, radial, depressed, slightly curved; wall thin, calcareous, composed of laminae of radial calcite, finely perforate; surface hispid; primary aperture interio-marginal, equatorial, broad low arch extending back along both umbilical margins to the septum; distinct porticus borders entire aperture, often obscuring parts of earlier

ZONE	Species																		
	Sample		Globotruncana concovata	G. linneiana coronata	G. culverensis	Planomalina ehrenbergi	Globotruncana marginata	G. linneiana linneiana	G. cretacea	Planomalina rowei	P. aspera	G. linneiana tricarinata	G. fornicata	G. cf. ventricosa	Planomalina multispina	Schackoina cushmani	Globotruncana rasetta	G. rugosa	G. arca
Belemnitella mucronata	C10						R	A			A	C			F	C		A	C
	C11						R	F			R	R				R		R	
	C13						R	R			C	C			R			R	
	C14							R			C	R	R						
	C17						R	F			F	F	F			R		R	
	C18						R	C			F	C	R			R		R	
	C19						R	R	A		F	F	C						
Marsupites - O. pilula - A. quadratus undifferentiated testudinarius	C21						R		F		C	C	C						
	C22						C	F	F		F	C	A	R			R		
	C23						A	R	A		C	C	A		R				
	C24						R	C	F		A	C	A		F		R		
	C25						F		R		F		R						
	C26						R		R		F								
	C27						C	F	A		C	C	A	R	R	?			
	C28						R	R	R		R	R	F						
	C29						F	R	A		C	R	F						
	C31						R		R		R								
	C32								R		R								
	C33								R	R	R								
	C34						R	R	R		R								
Micraster car-angulum	C35						R	R			F								
	C38										R								
	C40			R	F	C	R	C	R	C									
	C42	R	F		C	F	F	R	C	A	R								
	C43		F	F		C	F	F	R	C	R								
	C44		C	F		C	R	F	R	R	R								
	C45	R	C	R		C	F	F	R	R									
	C46	R	A	C		A	F	C		R									
	C47		C	F	R	F	F	C	R										
	C48	F	C	F	R	C	F	C											
	C49		F	R	R	F		C											
	C50	R	C		R	C	R	A											
A = abundant C = common F = few R = rare																			

TEXT-FIG. 4. Distribution of Foraminifera.

whorls; umbilical portions of apertures of successive chambers remain open as relict apertures; average maximum diameter 0.38 mm.

Remarks. Specimens of *P. aspera* from the Isle of Wight have been compared to topotypic specimens of *Globigerinella messinae messinae* Brönnimann at the University of Basel, and the two species were found to be very similar. *P. aspera*, however, is less compressed than *P. messinae messinae* (Brönnimann) and usually has 6 chambers in the final whorl while *P. messinae messinae* most commonly contains 5 chambers in its last whorl. The equatorial aperture of *P. messinae messinae* is usually much higher than that of *P. aspera*. Rare variants of *P. aspera* possess low double extraumbilical apertures caused by the convergence of the final chamber with the earliest chamber of the last whorl. None of the examined specimens, however, contain extraumbilical apertures which are as high as those of *Globigerinella biforaminata* Hofker.

Occurrence. *P. aspera* occurs in abundance in the Culver Cliff section and ranges from sample C46 in the lower *Micraster cor-anguinum* Zone to sample C10, the uppermost sample in the *Belemnitella mucronata* Zone. There are numerous recorded occurrences of this species in Senonian rocks from many areas of the world.

Planomalina ehrenbergi sp. nov.

Plate 69, figs. 1a, b

Description. Test free, planispiral with slightly trochoid initial whorl, biumbilicate, semi-evolute, periphery nearly circular, weakly lobulate, loosely coiled containing approximately $2\frac{1}{2}$ whorls; chambers globular to subglobular; final whorl contains 7 or 8 chambers; sutures radial, distinct, depressed, slightly curved; wall calcareous, thin, finely perforate; surface finely hispid; aperture interiomarginal, equatorial, a low arch extending back along both umbilical margins to the septum; thin porticus borders entire aperture and partially covers shallow umbilici; umbilical portion of apertures of successive chambers remain open as relict apertures.

Dimensions of holotype. Maximum diameter of holotype 0.27 mm.; maximum thickness 0.10 mm.

Remarks. *Planomalina ehrenbergi* has more chambers, is more compressed, not as lobulate, and not as coarsely hispid as the much more common *P. aspera*. *P. ehrenbergi* is more compressed and more nearly evolute than *P. aissana* (Sigal). The sutures of *P. ehrenbergi* are radial while those of *P. aissana* appear to be oblique.

Occurrence. *P. ehrenbergi* is fairly rare and is restricted to the *Micraster cor-testudinarium* and *Micraster cor-anguinum* Zones on the Isle of Wight.

Planomalina multispina (Lalicker)

Plate 69, figs. 5a, b

Biglobigerinella multispina Lalicker 1948, p. 624, pl. 92, figs. 1-3.

Biglobigerinella multispina Lalicker; Bolli, Loeblich, and Tappan 1957, p. 25, pl. 1, figs. 11-12.

Description. Test free, planispiral with slightly trochoid initial whorl, biumbilicate, semi-evolute, loosely coiled containing approximately 3 whorls, periphery circular,

lobulate; early chambers inflated, globular, final 1 to 3 chambers become broadly flattened and finally replaced by two paired globular chambers, one on each side of plane of coiling, 7 to 10 chambers in final whorl; sutures distinct, radial, slightly curved, depressed; wall calcareous perforate; surface hispid; primary apertures in final stage paired extraumbilical at base of each paired chamber, apertures extend back along both umbilical margins to septum, umbilical portions of apertures of successive chambers appear to remain open as relict apertures; portici poorly preserved; average maximum diameter 0.42 mm.

Remarks. Banner and Blow (1959, p. 9), in their classification of the superfamily *Globigerinaceae* (Carpenter), regard the genus *Biglobigerinella* Lalicker as a junior synonym of the genus *Globigerinelloides* Cushman and ten Dam, and have lowered the rank of *Globigerinelloides* to a subgeneric level. They place the subgenus *Globigerinelloides* within the genus *Planomalina* Loeblich and Tappan. In the present study, however, the taxon subgenus has not been used.

Planomalina multispina (Lalicker), the type species of *Biglobigerinella*, grades imperceptibly into *Planomalina aspera* (Ehrenberg) and may represent a late ontogenetic stage of *P. aspera*. These two forms are regarded as separate species in this study, however, as they appear to have different stratigraphic ranges on the Isle of Wight.

Occurrence. *P. multispina* is restricted to samples from the *Belemnitella mucronata* Zone and the *Actiuocamax quadratus* Zone (s.l.) at Culver Cliff. The holotype of *P. multispina* is from the Campanian of Arkansas.

Planomalina rowei sp. nov.

Plate 69, figs. 2a, b

Description. Test free, planispiral with slightly trochoid initial whorl, biumbilicate, semi-evolute, loosely coiled containing approximately 2 whorls; periphery somewhat rect-

EXPLANATION OF PLATE 69

Photographs retouched by author.

Fig. 1. *Planomalina ehrenbergi* sp. nov., holotype, $\times 125$. 1a, side view; 1b, edge view. *M. cor-anguinum* Zone, sample C42, P44608.

Fig. 2. *P. rowei* sp. nov., holotype, $\times 125$. 2a, side view; 2b, edge view. *M. cor-anguinum* Zone, sample C42, P44609.

Fig. 3. *Schackoina cushmani* sp. nov., paratype, $\times 125$. Side view; *B. mucronata* Zone, sample C10, P44625.

Fig. 4. *Planomalina aspera* (Ehrenberg), $\times 125$. 4a, side view; 4b, edge view. *M. cor-anguinum* Zone, sample C42, P44612.

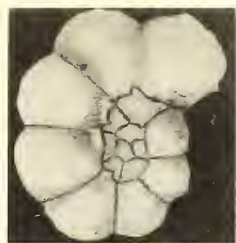
Fig. 5. *P. multispina* (Lalicker), $\times 88$. 5a, side view; 5b, edge view. *A. quadratus* Zone (s.l.), sample C24, P44626.

Fig. 6. *Globotruncana fornicata* Plummer, $\times 72$. 6a, dorsal view; 6b, side view; 6c, ventral view. *A. quadratus* Zone (s.l.), sample C24, P44623.

Fig. 7. *G. linneiana linneiana* (d'Orbigny), $\times 72$. 7a, dorsal view; 7b, side view; 7c, ventral view. *A. quadratus* Zone (s.l.), sample C27.

Fig. 8. *G. arca* (Cushman), $\times 72$. 8a, dorsal view; 8b, side view; 8c, ventral view. *B. mucronata* Zone, sample C10, P44621.

Fig. 9. *G. cretacea* (d'Orbigny), $\times 72$. 9a, dorsal view; 9b, side view; 9c, ventral view. *B. mucronata* Zone, sample C10, P44619.



1a



1b



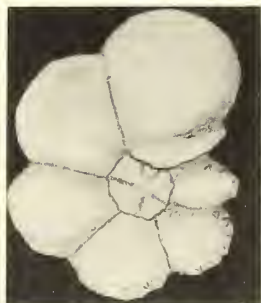
2a



2b



3



4a



4b



5a



5b



6a



6b



6c



7a



8a



8b



8c



7c



9a



9b



9c



7b

angular, lobulate; chambers subglobular to globular, final chamber radially elongate; final whorl contains $4\frac{1}{2}$ to 5 chambers; sutures distinct, radial, depressed, very slightly curved; wall calcareous, thin, finely perforate; surface finely hispid; umbilici shallow; aperture interiomarginal, equatorial, broad low arch extending back along both umbilical margins to the septum; porticus distinct, thin, borders entire aperture; umbilical portions of apertures of successive chambers remain open as relict apertures.

Dimensions of holotype. Maximum diameter of holotype 0.25 mm.; maximum thickness 0.11 mm.

Remarks. *Planomalina rowei* is distinguished from *P. aspera* (Ehrenberg) by its smaller size, fewer chambers, and its peripheral outline, which, due to the elongate final chamber, is somewhat rectangular, whereas in *P. aspera* it is circular or subcircular. *P. rowei* is smaller and less compressed than *P. messinae subcarinata* (Brönnimann), although they appear to have similar peripheral outlines.

Occurrence. *P. rowei* occurs commonly in the *Micraster cor-anguinum* Zone and is very rare in the *Marsupites testudinarius* Zone on the Isle of Wight.

Genus SCHACKOINA Thalmann 1932

Schackoina cushmani sp. nov.

Plate 69, fig. 3; text-figs. 5a-h

Description. Test free, nearly planispiral, loosely coiled, semi-evolute, biumbilicate; early chambers globular, radially elongate; final 1 or 2 chambers bulbous, almost polyhedral, 3 chambers in final whorl; 5 to 6 tubulospines from final whorl; earliest chamber of final whorl has 1 tubulospine, located in the median plane; second chamber has either 1 tubulospine located in the median plane or 2 tubulospines arranged on both sides of median plane; final chamber usually has 3 tubulospines, 1 located posteriorly in the median plane and the other 2 further forward on both sides of the median plane; sutures depressed, oblique, slightly curved; wall calcareous, thin, finely perforate; surface smooth; primary aperture interiomarginal, equatorial, a broad low arch; lip distinct, thin, borders entire aperture covering much of umbilici; umbilical portions of apertures of successive chambers appear to remain open as relict apertures; umbilici small, shallow.

Dimensions of holotype. Maximum diameter (excluding tubulospines) of holotype 0.22 mm.; thickness of umbilicus 0.05 mm.; thickness of final chamber 0.13 mm.

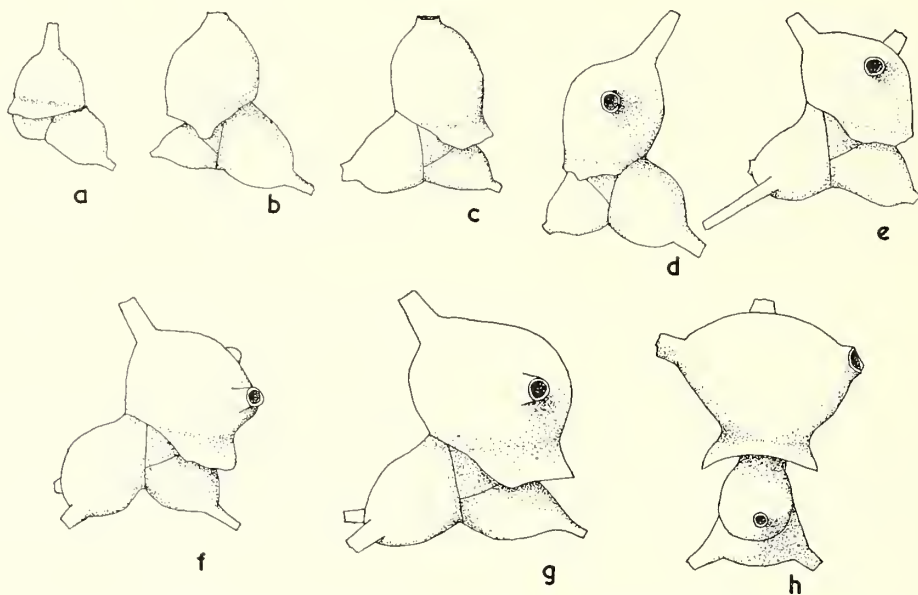
Remarks. *Schackoina cushmani* is morphologically similar to *S. multispinata* (Cushman and Wickenden) and may be closely related. *S. cushmani* differs from *S. multispinata*, however, in the following characters:

1. *S. cushmani* has a maximum development of 6 tubulospines from the final whorl compared to 7 tubulospines from the final whorl of the holotype of *S. multispinata*, and, furthermore, some specimens of *S. multispinata* have as many as 5 tubulospines from one chamber. Over 50 specimens of *S. cushmani* have been examined and only 1 specimen had over 6 tubulospines. This specimen had an extra tubulospine of

considerably smaller diameter which had penetrated the final chamber from an earlier whorl.

2. *S. cushmani* has a much larger and more prominent lip.
3. *S. multispinata* appears to be more involute (see Cushman and Wickenden 1930, pl. 6) than *S. cushmani*.

Young forms of *S. cushmani* somewhat resemble mature specimens of *S. trituberculata* (Morrow). Adult specimens of *S. cushmani*, however, have larger, more polyhedral,



TEXT-FIG. 5. *Schackoina cushmani* sp. nov. 5a-f, ontogenetic series of paratypes, P44624; 5g, side view of holotype, P44618; 5h, edge view of holotype. All illustrations are camera lucida drawings, $\times 160$. All specimens from sample C10 from the *Belemnitella mucronata* Zone.

final chambers. The holotype of *S. trituberculata* has 4 chambers in the final whorl while the final whorl of all examined specimens of *S. cushmani* contained only 3 chambers. *S. tappanae* Montanaro Gallitelli is similar to young specimens of *S. cushmani* and may represent an ancestral species. Adult specimens of *S. cushmani* are distinct, however, in having much more bulbous, nearly polyhedral, final chambers and by having 3 tubulospines on the final chamber.

Occurrence. *Schackoina cushmani* appears to be restricted to the *Belemnitella mucronata* Zone; however, two immature specimens of *Schackoina* were found in sample C27 from the *Actinocamax quadratus* Zone (s.l.) which may represent young forms of *S. cushmani* or a closely related species. This is the first recorded occurrence of the genus *Schackoina* from the British Isles.

Family GLOBOTRUNCANIDAE Brotzen 1942

Genus GLOBOTRUNCANA Cushman 1927

Globotruncana arca (Cushman)

Plate 69, figs. 8a-c

Pulvinulina arca Cushman 1926, p. 23, pl. 3, figs. 1a-c.*Globotruncana arca* (Cushman), Cushman 1927, p. 91, pl. 19, fig. 11.*Globotruncana arca* (Cushman), Cushman 1927a, p. 169, pl. 28, figs. 28a-c.*Globotruncana arca* (Cushman), Cushman and Todd 1943, p. 71, pl. 12, fig. 11.*Globotruncana arca* (Cushman), Cushman 1946 (part), p. 150, pl. 62, figs. 4a-c.*Globotruncana arca* (Cushman), Dalbiez 1955, text-figs. 5a-c.*Globotruncana arca* (Cushman), Brönnimann and Brown 1956, pp. 539-40, pl. 23, figs. 10-12.*Globotruncana arca* (Cushman), Edgell 1957, p. 110, pl. 1, figs. 10-12; pl. 3, figs. 4-6.*Globotruncana arca* (Cushman), Bolli, Loeblich, and Tappan 1957, p. 44, pl. 11, figs. 6-11.

Description. Test free, low trochospiral, biconvex, evolute, umbilicate, $2\frac{1}{2}$ to 3 whorls, equatorial periphery nearly circular, lobulate with 2 well-developed, subparallel, beaded keels; dorsal keel diverges on to spiral side of test as dorsal sutural ridge; ventral keel diverges to umbilical side of terminal chamber face usually not coinciding precisely with ventral suture and then extends back along the umbilical margin as slightly raised ridge; chambers angular truncate, inflated ventrally, 6 to 8 chambers in final whorl uniformly increasing in size; dorsal sutures distinct, oblique, strongly curved, raised; ventral sutures distinct, nearly radial, slightly curved, depressed in late chambers, flush or raised in early portion of test; umbilicus moderately broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, perforate except for imperforate keels, peripheral area between keels, and tegilla; chamber surfaces weakly hispid; all 20 examined specimens coiled dextrally; average maximum diameter 0.52 mm.

Remarks. Specimens from the Isle of Wight are slightly less convex ventrally than the holotype of *G. arca*, and the keels may be more closely spaced. Nevertheless, these specimens appear to be within the range of variation of *G. arca*.

Occurrence. *G. arca* is rare in the samples studied from Culver Cliff, occurring only in the uppermost sample, C10, from the *Belemnitella mucronata* Zone. Two specimens similar to *G. arca* were found about 82 feet lower in the same zone in sample C17. These forms were less convex dorsally and their chambers were more elongate in the direction of coiling than *G. arca* (s.s.). The holotype of *G. arca* is from the upper portion of the Papagallos shale (Maestrichtian), San Luis Potosi, Mexico. Bolli (1957, p. 53) records *G. arca* in Trinidad from the Campanian and Lower Maestrichtian. Brönnimann and Brown (1956, p. 540) believe *G. arca* (s.s.) to be restricted to Maestrichtian strata. There are, however, numerous reported occurrences of this species from Campanian strata from many parts of the world.

Globotruncana cretacea (d'Orbigny)

Plate 69, figs. 9a-c; Plate 72, fig. 6

Globigerina cretacea d'Orbigny 1840, p. 34, pl. 3, figs. 12-14.*Globigerina cretacea* d'Orbigny var. *saratogaensis* Applin, in Applin, Ellisor, and Kniker 1925, p. 98, pl. 3, figs. 8a-c.

Globotruncana globigerinoides Brotzen 1936, p. 177, pl. 12, figs. 3a-c; pl. 13, fig. 3.

Rosalinella globigerinoides (Brotzen), Schijfsma 1946, p. 96, pl. 7, figs. 9a-c.

Globotruncana saratogaensis (Applin), Brönnimann and Brown 1956, pp. 544-5, pl. 21, figs. 1-3.

Globigerina cretacea d'Orbigny; Banner and Blow 1960, pp. 8-10, pl. 7, figs. 1a-c.

Description. Test free, low trochospiral, slightly biconvex, evolute, umbilicate, $2\frac{1}{2}$ to 3 whorls, equatorial periphery nearly circular, lobulate with 2 weakly developed keels, often indistinct on late chambers; chambers inflated, globular, slightly elongate in direction of growth, 5 to 6 chambers in final whorl uniformly increasing in size; sutures distinct, depressed, nearly radial, slightly oblique in late chambers; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with accessory apertures; primary aperture interiomarginal, umbilical; surface of first two whorls coarsely hispid, surface of final 2 or 3 chambers finely hispid; coiling predominantly dextral; 91 of 100 specimens selected randomly coiled dextrally; average maximum diameter 0.46 mm.

Remarks. The test wall of *G. cretacea* is thinner than that of any other species of *Globotruncana* in this study and consists of numerous laminae of calcite. This species appears to be especially susceptible to recrystallization. Although the test wall of a few of the examined specimens shows a poorly preserved radial arrangement of calcite crystals, most specimens exhibit a finely granular wall structure which is undoubtedly the result of diagenetic change. The peripheral portion of the test wall between the keels appears to be imperforate or, at least, less perforate than the remainder of the test wall. The keels are usually not discernible in thin section. It is suggested that *G. cretacea* may be a transition species between the genera *Globotruncana* and *Rugoglobigerina*.

In the original description of *Globigerina cretacea*, d'Orbigny (1840) does not mention the presence of keels or tegilla. Banner and Blow (1960, p. 8) re-examined d'Orbigny's material from the Lower Campanian White Chalk of St. Germain, near Paris, and designated a lectotype of *G. cretacea* from a syntypic series. The lectotype possesses two broadly spaced but weakly developed keels, and it is suggested, considering the optical instruments available in 1840, that d'Orbigny overlooked this faintly defined feature. Other specimens from d'Orbigny's collections which were 'clearly conspecific with the lectotype' possessed well-preserved tegilla. The presence of keels and tegilla indicates that this species should be placed in the genus *Globotruncana* Cushman.

Brotzen (1936, p. 177) regarded *Globotruncana globigerinoides* morphologically similar to *Globigerina cretacea*, but because *G. globigerinoides* possessed a weakly developed double keel these two species were considered distinct. Banner and Blow's observation of a weak double keel on d'Orbigny's specimens of *Globigerina cretacea* indicates that these two species are probably conspecific.

Specimens from this current study have been compared to specimens of *Globigerina cretacea* in the collections of Alcide d'Orbigny in the Muséum National de l'Histoire Naturelle, Paris, France, and were found to be conspecific.

Occurrence. Banner and Blow (op. cit., p. 10) state: 'With the evidence available to us we consider that *Globotruncana cretacea* (d'Orbigny) is limited in range from the Coniacian to Campanian, with the possibility of its occurrence in the highest Turonian. It is also possible that typical forms with the weak carinae do not occur above the

Lower Campanian.' This species occurs commonly throughout the studied Culver Cliff section, the uppermost part of which is Upper Campanian in age.

Globotruncana concavata (Brotzen)

Plate 71, figs. 4a-c

Rotalia concavata Brotzen 1934, p. 66, pl. 3, fig. b.

Globorotalia asymetrica Sigal 1952, p. 35, fig. 35.

Globotruncana (*Globotruncana*) *ventricosa ventricosa* (not White), Dalbiez 1955, p. 168, text-figs. 7a-d.

Globotruncana concavata (Brotzen), Bolli 1957, p. 57, pl. 13, figs. 3a-c.

Description. Test free, very low trochospiral, dorsal side flat to slightly concave, ventral side strongly convex, evolute, umbilicate, $2\frac{1}{2}$ to 3 whorls, equatorial periphery nearly circular, weakly lobulate, with 2 well-developed, very closely spaced, finely beaded keels; dorsal keel diverges on to spiral side of test as slightly raised sutural ridge; ventral keel diverges to umbilical side of terminal chamber face usually not coinciding precisely with ventral suture and usually not completely visible on ventral side of test because of slightly embracing nature of chambers, ventral keel then extends back along umbilical margin as an indistinct weakly raised ridge; chambers hemispherical, 5 to 6 chambers in final whorl uniformly increasing in size; dorsal sutures distinct, oblique, strongly curved, slightly raised, finely beaded; ventral sutures distinct, radial, depressed; umbilicus moderately broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, perforate except for imperforate keels, peripheral area between keels, and tegilla; dorsal surface weakly hispid to smooth; ventral surface coarsely hispid becoming less hispid with growth; all of limited number of specimens coiled dextrally; approximate diameter 0.58 mm.

Remarks. *G. concavata* is quite similar to *Globotruncana ventricosa* White in general appearance. Bolli (1957, p. 57, pl. 13, figs. 3 a-c, 4a-c) has examined topotype specimens of both species and offers a pertinent discussion and excellent illustrations of *G. concavata* and *G. ventricosa*. *G. concavata* is usually flat to concave dorsally while the dorsal side of *G. ventricosa* is flat to slightly convex. The dorsal sutures of *G. ventricosa* are much more strongly raised and thicker than those of *G. concavata*.

Occurrence. *G. concavata* is rare and is restricted in the samples studied to the *Micraster cor-anguinum* and *Micraster cor-testudinarium* Zones. This occurrence agrees well with that reported by Bolli (loc. cit.) who states, '*Globotruncana concavata* appears to be restricted to the upper part of the Coniacian and Lower Santonian, . . . '.

Globotruncana culverensis sp. nov.

Plate 71, figs. 1a-c

Description. Test free, low trochospiral, slightly biconvex, evolute, umbilicate, 3 to $3\frac{1}{2}$ whorls, equatorial periphery nearly circular, lobulate with 2 fairly well-developed, closely spaced, finely beaded keels which often merge into single keel on final 1 to 4 chambers; dorsal keel extends on to spiral side of test as slightly raised sutural ridge;

ventral keel diverges on to umbilical side of test and is often obscured by embracing nature of chambers, then extends back along umbilical margin as a slightly raised ridge; chambers inflated, slightly truncate, slightly elongate in direction of coiling, overlapping, 7 to 8 chambers in final whorl uniformly increasing in size, often added in slightly oblique position; sutures distinct, depressed, nearly radial; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, uniformly perforate except for imperforate keels, peripheral area between keels, and tegilla; surface hispid becoming less hispid with growth; coiling predominantly dextral; 29 of 30 specimens selected at random coiled dextrally.

Dimensions of holotype. Maximum diameter of holotype 0.74 mm.; maximum thickness 0.27 mm.

Remarks. Immature specimens of *G. culverensis* are almost identical to more mature specimens of *G. marginata* (Reuss) and there is a gradation of forms between these two species. Mature specimens of *G. culverensis* are quite distinct, however, having 7 or 8 chambers and being much larger than *G. marginata* which usually has 5 or 6 chambers. *G. marginata* has a double keel on the periphery of all of its chambers while the double keel of *G. culverensis* usually merges into a single dichotomous keel on the periphery of the final 1 to 4 chambers. These two species have different stratigraphic ranges, and although the true lower limits of the stratigraphic ranges of both species are not known from this study, it is suggested that *G. culverensis* was derived from *G. marginata*.

Occurrence. In the studied samples *G. culverensis* is restricted to the *Micraster cor-anguinum* and *Micraster cor-testudinarium* Zones while *G. marginata* ranges into the *Belemnitella mucronata* Zone.

Globotruncana fornicata Plummer

Plate 69, figs. 6a-c; Plate 72, figs. 1, 2

Globotruncana fornicata Plummer 1931, p. 198, pl. 13, figs. 4a-c, 5, 6.

Globotruncana fornicata Plummer, Sandidge 1932, p. 285, pl. 44, figs. 12-13.

Globotruncana fornicata Plummer, Cushman and Hedberg 1941, p. 99, pl. 23, figs. 18a-c.

Globotruncana fornicata Plummer, Cushman and Deaderick 1944, p. 340, pl. 53, figs. 28a-b.

Globotruncana fornicata Plummer, Cushman 1946, p. 149, pl. 61, figs. 19a-c.

Globotruncana fornicata Plummer, Cita 1948, p. 153, pl. 3, figs. 8a-c.

Globotruncana fornicata Plummer, Hagn 1953, p. 98, pl. 8, figs. 8a-c; text-figs. 22, 23.

Globotruncana fornicata Plummer, Frizzell 1954, p. 129, pl. 20, figs. 26a-c.

Globotruncana fornicata Plummer, Brönnimann and Brown 1956, pp. 542-4, pl. 21, figs. 7, 14, 15.

Globotruncana fornicata Plummer, Edgell 1957, p. 112, pl. 3, figs. 10-12.

Description. Test free, low to moderately high trochospiral, dorsal side convex, ventral side flat to slightly convex, evolute, umbilicate, $2\frac{1}{2}$ to 3 whorls; equatorial periphery circular, slightly lobulate with 2 well-developed, finely beaded keels, closely spaced and slightly diverging anteriorly, keels on early portion of chamber more closely spaced than on late portion of preceding chamber producing a 'cone in cone' arrangement, but, in general, becoming progressively more closely spaced with growth; dorsal keel extends on to spiral side of test as sutural ridge; ventral keel diverges to umbilical side

of terminal chamber face forming sutural ridge and then extends back along umbilical margin as a slightly raised ridge; chambers angular truncate, strongly curved, elongate in direction of growth, $4\frac{1}{2}$ to 6 chambers in final whorl, somewhat irregularly increasing in size; sutures distinct, oblique, strongly curved, raised, beaded; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, uniformly perforate except for imperforate keels, peripheral area between keels, and tegilla; surface weakly hispid; coiling predominantly dextral; 220 of 226 specimens selected at random coiled dextrally; average maximum diameter 0.54 mm.

Remarks. *Globotruncana fornicata* exhibits considerable variation. Many specimens are higher spired dorsally than Plummer's figured holotype, but none is as high spired as the possibly related *Globotruncana contusa* Cushman. The 'cone in cone' arrangement of the keels and the broadly curved chambers of *G. fornicata* clearly distinguish this species from most other double keeled *Globotruncana*.

Occurrence. This species, although in abundance, appears to be restricted on the Isle of Wight to the *Actinocamax quadratus* Zone (s.l.) and the lower part of the *Belemnitella mucronata* Zone. The holotype of *G. fornicata* is from the Upper Taylor formation (L. Campanian ?) of south-eastern Texas. Bolli (1957, p. 53) lists the range of *G. fornicata* in Trinidad as Santonian to possibly Lower Maestrichtian. Cita (1948, p. 153) records the range of this species in Italy as Santonian to Maestrichtian.

Globotruncana linneiana linneiana (d'Orbigny)

Plate 69, figs. 7a-c; Plate 72, fig. 5

Rosalina linneiana d'Orbigny 1839, p. 101, pl. 5, figs. 10-12.

Rosalina linnei d'Orbigny, type 1, de Lapparent 1918, p. 4, figs. a, c.

Globotruncana lapparenti Brotzen 1936, p. 175.

Globotruncana linnei (d'Orbigny), Renz 1936, pl. 6, figs. 32-34.

Globotruncana linnei (d'Orbigny), Gandolfi 1942, pp. 125-30, pl. 3, fig. 3; pl. 4, figs. 18, 32, 33.

Globotruncana linnei typica Vogler 1941, p. 286, pl. 23, figs. 12-21.

Globotruncana lapparenti lapparenti Brotzen, Bolli 1945, p. 230, pl. 9, fig. 11; text-fig. 1, nos. 15-16.

Globotruncana canaliculata (Reuss), Cushman 1946 (part), p. 149, pl. 61, figs. 17a-c.

Globotruncana lapparenti lapparenti Brotzen, Cita 1948, pp. 155-6, pl. 4, figs. 2a-c.

Globotruncana lapparenti Brotzen, Reichel 1950, p. 613, pl. 16, fig. 9; pl. 17, fig. 9.

Globotruncana lapparenti lapparenti Brotzen, Hagn 1953, p. 96, pl. 8, fig. 12; text-figs. 16-17.

Globotruncana lapparenti lapparenti Brotzen, Hagn and Zeil 1954, pp. 39-42, pl. 3, fig. 3; pl. 6, figs. 5, 8.

Globotruncana linneiana (d'Orbigny), Brönnimann and Brown 1956, pp. 540-2, pl. 20, figs. 13-17; pl. 21, figs. 16-18.

Globotruncana lapparenti lapparenti Brotzen, Edgell 1957, p. 113, pl. 1, figs. 7-9.

Description. Test free, very low trochospiral, both sides flat to slightly convex, evolute, umbilicate, 3 to $3\frac{1}{2}$ whorls; equatorial periphery circular, slightly lobulate with 2 well-developed, broadly spaced, subparallel, beaded keels; dorsal keel diverges slightly to dorsal side extending on to spiral surface of test as dorsal sutural ridge; ventral keel diverges to umbilical side of terminal chamber face forming ventral sutural ridge and then extends back along umbilical margin as a slightly raised ridge; chambers slightly

angular truncate, 6 to 6½ chambers in final whorl uniformly increasing in size; dorsal sutures distinct, oblique, strongly curved, raised, beaded; ventral sutures distinct, slightly oblique, curved, slightly raised, beaded; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, uniformly perforate except for imperforate keels, peripheral area between keels, and tegilla; chamber surfaces weakly hispid; coiling predominantly dextral; 59 of 60 specimens selected at random coiled dextrally; average maximum diameter 0.50 mm.

Remarks. Bolli (1951, p. 191) discussed the taxonomic problems of this group of *Globotruncanae*. He suggested, although it is possible that the poorly known species *Rosalina canaliculata* Reuss 1854 and *R. marginata* Reuss 1845 may be synonymous with *R. linneiana* d'Orbigny 1839, that for the purpose of convenience and simplification until the taxonomic problems regarding these species are clarified all double-keeled specimens which fulfil the general requirements of this group be regarded as subspecies of *Globotruncana lapparenti* Brotzen.

Brönnimann and Brown (1956, pp. 540–2) have proposed a neotype for *Rosalina linneiana* d'Orbigny from topotypic material. They tentatively regard *R. linneiana* as conspecific with *R. canaliculata*, and treat *Globotruncana lapparenti* as a distinct species. They consider *R. linneiana* more compressed ventrally than *G. lapparenti*. The present author, however, considers *R. linneiana* conspecific with *G. lapparenti* lapparenti Brotzen emend. Bolli which is one of the more ventrally compressed subspecies of the 'lapparenti' group. *G. lapparenti* is, therefore, a junior synonym of *R. linneiana*, and the subspecies of *G. lapparenti* should be considered subspecies of *R. linneiana*.

Occurrence. *Globotruncana linneiana linneiana* occurs commonly throughout the studied Culver Cliff section. Bolli's (1945, p. 230) specimens of *G. lapparenti lapparenti* (= *G. linneiana linneiana*) from Switzerland range from the Turonian to the Campanian. Bolli (1957, p. 53) indicates on his range chart that *G. lapparenti lapparenti* is restricted in Trinidad to Santonian and Campanian strata.

Globotruncana linneiana coronata Bolli

Plate 70, figs. 1a–c; Plate 72, figs. 3, 4

Rosalina linnei d'Orbigny, type 4 de Lapparent 1918, p. 4, fig. 1g.

Globotruncana lapparenti coronata Bolli 1945, p. 233, pl. 9, figs. 14–15; text-fig. 1, nos. 21–22.

Globotruncana lapparenti coronata Bolli, Cita 1948, p. 156, pl. 4, fig. 3.

Globotruncana lapparenti coronata Bolli, Mornod 1950, pp. 591–2, text-figs. 13a–d.

EXPLANATION OF PLATE 70

All illustrations ×72. Photographs retouched by author.

Fig. 1. *Globotruncana linneiana coronata* Bolli. 1a, dorsal view; 1b, side view; 1c, ventral view. *M. cor-anguinum* Zone, sample C47, P44607.

Fig. 2. *G. linneiana tricarinata* (Quereau). 2a, dorsal view; 2b, side view; 2c, ventral view. *B. mucronata* Zone, sample C10, P44606.

Fig. 3. *G. marginata* (Reuss). 3a, dorsal view; 3b, side view; 3c, ventral view. *A. quadratus* Zone (s.l.), sample C24, P44622.

Fig. 4. *G. rosetta* (Carsey). 4a, dorsal view; 4b, side view; 4c, ventral view. *A. quadratus* Zone (s.l.), sample C22, P44617.



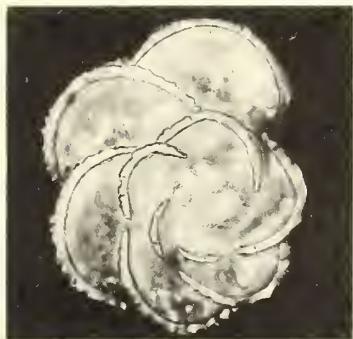
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1b



1c



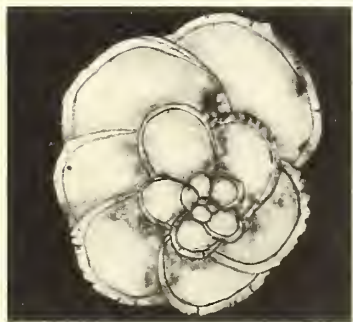
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2b



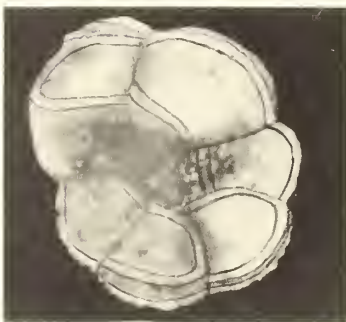
2c



3a



3b



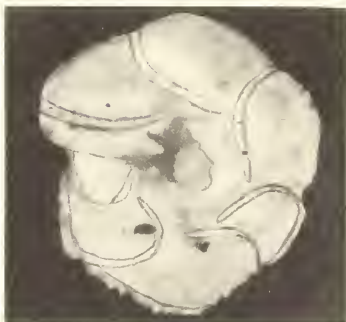
3c



4a



4b



4c

Globotruncana lapparenti coronata Bolli, Hagn and Zeil 1954, pp. 43-44, pl. 3, fig. 4; pl. 7, figs. 1-3.

Description. Test free, very low trochospiral, dorsal side slightly convex to flat, ventral side moderately to slightly convex, evolute, umbilicate, 3 to $3\frac{1}{2}$ whorls; equatorial periphery circular, slightly lobulate with 2 well-developed, subparallel, beaded keels, broadly spaced on early chambers, more closely spaced on final chambers; dorsal keel extends on to spiral surface of test as dorsal sutural ridge; ventral keel diverges to umbilical side of terminal chamber face forming ventral sutural ridge and then extends back along the umbilical margin as a slightly raised ridge; chambers angular truncate, 6 to 9 chambers in final whorl, uniformly and rapidly increasing in size; dorsal sutures distinct, oblique, strongly curved, raised, beaded; ventral sutures distinct, slightly oblique, curved, raised, beaded; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, uniformly perforate except for imperforate keels, peripheral area between keels, and tegilla; chamber surfaces weakly hispid; coiling predominantly dextral; 88 randomly selected specimens were all coiled dextrally; average maximum diameter 0.64 mm.

Remarks. *G. linneiana coronata* is larger and usually has more chambers than *G. linneiana linneiana* or *G. linneiana tricarinata*. The double keels of *G. linneiana coronata* are usually more closely spaced than those of the other two subspecies, and the chambers are more compressed ventrally than those of *G. linneiana tricarinata*.

Occurrence. *G. linneiana coronata*, although in abundance, is restricted in the samples studied to the *Micraster cor-anguinum* and *Micraster cor-testudinarium* Zones. Bolli's (1945) specimens of this subspecies from Switzerland were from Turonian, Coniacian, and Santonian beds. Cita (1948, p. 156) reports the range for *G. lapparenti coronata* in Italy as Turonian to Santonian.

Globotruncana linneiana tricarinata (Quereau)

Plate 70, figs. 2a-c

Pulvinulina tricarinata Quereau 1893, pl. 5, fig. 3a.

Rosalina linnei (d'Orbigny), type 2 de Lapparent 1918, p. 4, figs. 1b, d, e, f; p. 5, figs. 2d, n.

Globotruncana linnei (d'Orbigny), Renz 1936 (part), p. 19, pl. 6, figs. 28-30; pl. 8, fig. 7.

Globotruncana linnei tricarinata (Quereau), Vogler 1941, pl. 23, figs. 22-31.

Globotruncana lapparenti tricarinata (Quereau), Bolli 1945, pp. 232-3, pl. 9, fig. 13; text-fig. 1, nos. 19, 20.

Globotruncana canaliculata (Reuss), Cushman 1946 (part), p. 149, pl. 61, figs. 18a-c.

Globotruncana lapparenti tricarinata (Quereau), Cita 1948, pp. 157-8, pl. 4, figs. 4a-c.

Globotruncana lapparenti tricarinata (Quereau), Hagn and Zeil 1954, pp. 42-43, pl. 6, figs. 6-7.

Description. Test free, very low trochospiral, dorsal side slightly convex to flat, ventral side moderately to slightly convex, evolute, umbilicate, 3 to $3\frac{1}{2}$ whorls; equatorial periphery circular, lobulate with 2 well-developed, broadly spaced, subparallel, beaded keels; dorsal keel diverges slightly to dorsal side extending on to spiral surface of test as dorsal sutural ridge; ventral keel diverges to umbilical side of terminal chamber face forming ventral sutural ridge and then extends back along umbilical margin as a slightly

raised ridge; chambers angular truncate, ventrally inflated, 6 chambers in final whorl uniformly increasing in size; dorsal sutures distinct, oblique, strongly curved, raised, beaded; ventral sutures distinct, slightly oblique, curved, flush to slightly raised, beaded; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, uniformly perforate except for imperforate keels, peripheral area between keels, and tegilla; chamber surfaces weakly hispid; coiling predominantly dextral; 140 of 142 specimens selected at random coiled dextrally; average maximum diameter 0.54 mm.

Remarks. *G. linneiana tricarinata* differs from *G. linneiana linneiana* in being ventrally more convex. The chambers of *G. linneiana tricarinata* are ventrally inflated while the chambers of *G. linneiana linneiana* are more compressed.

Occurrence. This subspecies is very rare in the *Micraster cor-anguinum* Zone and occurs commonly in the *Actinocamax quadratus* Zone (s.l.) and the *Belemnitella mucronata* Zone at Culver Cliff. Bolli (1945) records the range of *G. lapparenti tricarinata* (= *G. linneiana tricarinata*) in Switzerland as Turonian to Maestrichtian, and Cita (1948, p. 157) also reports a Turonian to Maestrichtian range for *G. lapparenti tricarinata* in Italy. Bolli (1957, p. 53), however, lists on a range chart a more restricted range of Campanian to L. Maestrichtian for *G. lapparenti tricarinata* in Trinidad.

Globotruncana marginata (Reuss)

Plate 70, figs. 3a-c; Plate 72, figs. 7, 8a-c

Rosalina marginata Reuss 1845, p. 36, pl. 13, fig. 68.

Rosalina marginata Reuss, Reuss 1854, p. 59, pl. 26, fig. 1.

Globigerina marginata (Reuss), Loetterle 1937, pp. 44-45, pl. 7, fig. 3.

Globotruncana linnei bulloides Vogler 1941, p. 287, pl. 23, figs. 32-39.

Globotruncana lapparenti bulloides Vogler, Bolli 1945, pp. 231-2, text-fig. 1 (17-18); pl. 19, fig. 12.

Rosalinella marginata (Reuss), Schijfsma 1946, p. 97, pl. 7, figs. 10a-c.

Globotruncana marginata (Reuss), Cushman 1946, p. 150, pl. 62, figs. 1-2.

Globotruncana marginata (Reuss), Hagn 1953, p. 93, pl. 8, fig. 10; text-figs. 10, 11.

Globotruncana marginata (Reuss), Hagn and Zeil 1954, pp. 46-47, pl. 2, fig. 4; pl. 7, figs. 5, 6.

Globotruncana marginata (Reuss), Frizzell 1954, p. 129, pl. 20, fig. 24.

Globotruncana marginata (Reuss), Edgell 1957, p. 114, pl. 2, figs. 4-6.

Description. Test free, very low trochospiral, slightly biconvex, evolute, umbilicate, $2\frac{1}{2}$ to 3 whorls, equatorial periphery nearly circular, lobulate, with 2 weakly to fairly well-developed, closely spaced, finely beaded, keels; dorsal keel diverges obliquely on

EXPLANATION OF PLATE 71

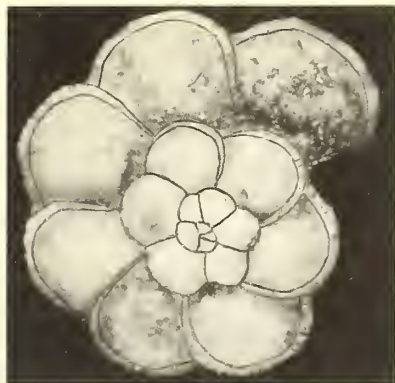
All illustrations $\times 72$. Photographs retouched by author.

Fig. 1. *Globotruncana culverensis* sp. nov., holotype. 1a, dorsal view; 1b, side view; 1c, ventral view. *M. cor-anguinum* Zone, sample C46, P44602.

Fig. 2. *G. cf. ventricosa* White. 2a, dorsal view; 2b, side view; 2c, ventral view. *A. quadratus* Zone (s.l.), sample C27, P44616.

Fig. 3. *G. rugosa* (Marie). 3a, dorsal view; 3b, side view; 3c, ventral view. *B. mucronata* Zone, sample C10.

Fig. 4. *G. concavata* (Brotzen). 4a, dorsal view; 4b, side view; 4c, ventral view. *M. cor-anguinum* Zone, sample C42, P44615.



1a



1b



1c



2a



2b



2c



3a



3b



3c



4a



4b



4c

to spiral side of test forming a sutural ridge in early portion of test, on later chambers dorsal keel does not always coincide precisely with dorsal sutures; ventral keel, sometimes more weakly developed than dorsal keel, diverges to umbilical side of terminal chamber face commonly coinciding with ventral sutures of early chambers, on later chambers ventral keel usually does not coincide precisely with ventral sutures and often ventral keel is not completely visible on the umbilical side of test because of embracing nature of chambers, ventral keel extends back along umbilical margin as a slightly raised, indistinct ridge; chambers inflated, slightly truncate, elongate in direction of coiling, overlapping, 5 to 6 chambers in final whorl uniformly increasing in size, chambers often added in slightly oblique position; sutures of late chambers distinct, slightly oblique, curved, usually depressed, rarely raised; sutures on early chambers distinct, slightly oblique, curved, slightly raised or flush, finely beaded; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, uniformly perforate except for imperforate keels, peripheral area between keels, and tegilla; surface weakly hispid; coiling predominantly dextral; 185 of 190 specimens selected at random coiled dextrally; average maximum diameter 0.54 mm.

Remarks. Because of the inadequacy of Reuss's original description and illustration, there has been much confusion as to the nature of *G. marginata*. Bolli *et al.* (1957, p. 46) have discussed some of the problems arising from the poorly known type and have designated a specimen originally illustrated by Reuss (1845, pl. 13, fig. 68) which most closely corresponds to the original written description as the lectotype. The illustration of the designated lectotype, however, is very small and does not show the morphology necessary to recognize the species. Cushman (1946, p. 150), after examining specimens of *G. marginata* from the collections of Reuss in Dresden, Vienna, and Cambridge, reported that they were all in agreement and figures (op. cit., pl. 62, figs. 1a-c) a specimen of *G. marginata* from Reuss's Cambridge collection.

Occurrence. *G. marginata* is fairly abundant in the studied samples from Culver Cliff and occurs from the *M. cor-testudinarium* Zone to the lower part of the *Belemnitella mucronata* Zone. The specimen proposed by Bolli *et al.* (1957, p. 46) as the lectotype of *G. marginata* is from the Turonian of Bohemia. Edgell (1957, p. 114) states that within the Carnarvon Basin of North-western Australia, *G. marginata* appears to be restricted to beds of Santonian and Campanian age.

Bolli's hypotype (1945, pl. 9, fig. 12) of *Globotruncana lapparenti bulloides* has been examined by the present author at the Geological Institute, University of Zurich, and is believed to be a slightly oblique section of *G. marginata*. Bolli (op. cit.) reports the range of *G. lapparenti bulloides* in Switzerland as Turonian to L. Santonian.

Globotruncana rosetta (Carsey)

Plate 70, figs. 4a-c

Globigerina rosetta Carsey 1926, p. 44, pl. 5, figs. 3a-c.

Globotruncana rosetta (Carsey), Brönnimann and Brown 1956, p. 545, pl. 21, figs. 11-13.

Description. Test free, very low trochospiral, dorsal side slightly convex, ventral side strongly convex, evolute, umbilicate, $2\frac{1}{2}$ to 3 whorls; equatorial periphery circular,

slightly lobulate with a single dichotomous or 2 very closely spaced, beaded keels on the early chambers and a single keel on final chambers; dorsal keel extends on to spiral side of test as dorsal sutural ridge; ventral keel extends on to umbilical side of test and along umbilical margin as a slightly raised ridge; chambers hemispherical, 6 to 7 chambers in final whorl uniformly increasing in size; dorsal sutures distinct, oblique, strongly curved, raised, beaded; ventral sutures distinct, oblique, curved, slightly raised or flush; umbilicus moderately broad, in well-preserved specimens covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, not examined in thin section; surface weakly hispid; all of limited number of specimens coiled dextrally; average maximum diameter 0.54 mm.

Remarks. In the original description of *G. rosetta*, Carsey (1926, p. 44) did not mention the presence of a double keel and presented no illustration of a peripheral view of this specimen. Brönnimann and Brown (1956, p. 546), however, state: 'Examination of the holotype of *Globotruncana rosetta* (Carsey), in the Carsey Collection at the University of Texas, reveals that it possesses two keels in the early chambers of the last whorl which are very close together. In the ante- and penultimate chambers the keels join.'

In the light of Brönnimann and Brown's re-examination of the holotype, it is necessary to critically re-examine all specimens referred in the literature to *G. rosetta* (Carsey).

Occurrence. Specimens of *G. rosetta* (Carsey) are very rare, found only in samples C22 and C24 from the *Actinocamax quadratus* Zone (s.l.). Brönnimann and Brown (op. cit., p. 546) report the range of this species as Campanian to Maestrichtian.

Globotruncana rugosa (Marie)

Plate 71, figs. 3a-c

Rosalinella rugosa Marie 1941, p. 241, pl. 35, fig. 340.

Globotruncana rugosa (Marie), Hagn 1953, pl. 8, fig. 13.

Description. Test free, trochospiral, moderately biconvex, evolute, umbilicate, $2\frac{1}{2}$ to 3 whorls, equatorial periphery subcircular, weakly lobulate with 2 well-developed, widely to closely spaced, beaded keels; dorsal keel diverges on to spiral side of final whorl as strongly raised sutural ridges, but not apparent on dorsal side of early whorls; ventral keel extends on to umbilical side of test not precisely coinciding with ventral

EXPLANATION OF PLATE 72

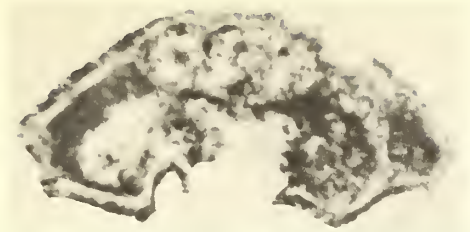
Figs. 1, 2. *Globotruncana fornicata* Plummer. 1, axial section, P44596, $\times 112$. 2, axial section, P44597, $\times 112$. Both specimens from *A. quadratus* Zone (s.l.), sample C22.

Figs. 3, 4. *G. linneiana coronata* Bolli. 3, axial section, $\times 112$. *M. cor-anguinum* Zone, sample C47, P44600. 4, axial section, $\times 112$. *M. cor-anguinum* Zone, sample C46, P44599.

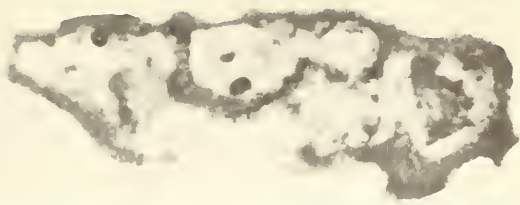
Fig. 5. *G. linneiana linneiana* (d'Orbigny), $\times 112$. Axial section. *M. cor-anguinum* Zone, sample C46, P44601.

Fig. 6. *G. cretacea* (d'Orbigny), $\times 112$. Axial section. Keels are not usually apparent in thin section. *B. mucronata* Zone, sample C10, P44598.

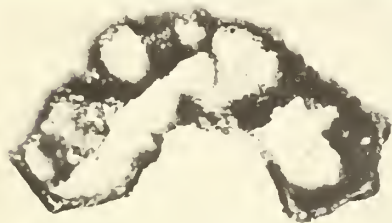
Figs. 7, 8. *G. marginata* (Reuss). 7, axial section, P44595, $\times 112$. 8a, axial section, P44595, $\times 112$; 8b, peripheral portion of final chamber showing perforate and imperforate parts of test wall, $\times 750$ approx.; 8c, lower half of same portion of test wall using polarized light showing radial wall structure of both perforate and imperforate parts of test, $\times 1400$ approx. Both specimens from *M. cor-anguinum* Zone, sample C46.



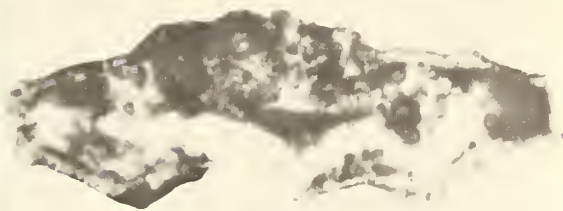
1



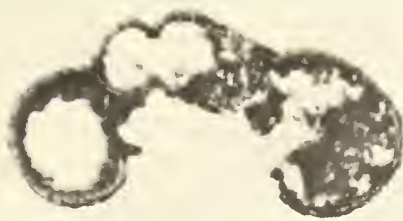
3



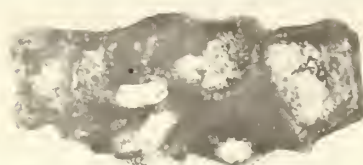
2



4



6



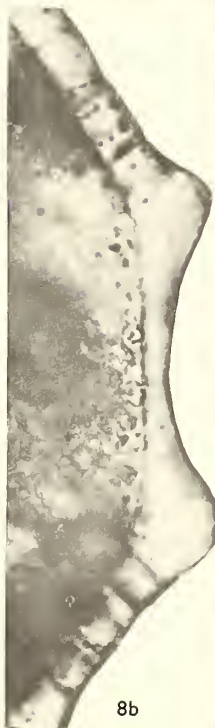
5



7



8a



8b



8c

sutures then extends back along umbilicus as fairly prominent ridge; chambers strongly curved, truncate, inflated ventrally, latest 1 to 4 chambers often depressed dorsally, 5 to $6\frac{1}{2}$ chambers in final whorl uniformly increasing in size; dorsal sutures of final 1 to $1\frac{1}{2}$ whorls distinct, strongly curved, beaded, raised; early dorsal sutures indistinct, depressed, slightly oblique; ventral sutures distinct, depressed, slightly oblique; umbilicus broad, deep, in well-preserved specimens covered by a complex tegillum with accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous, composed of radial calcite, perforate except for imperforate keels, peripheral area between keels, and tegilla; surface of initial 1 to 2 whorls weakly rugose, final whorl coarsely hispid; coiling predominantly dextral; 28 of 30 specimens selected at random coiled dextrally; approximate maximum diameter 0.54 mm.

Remarks. *Globotruncana rugosa* appears to have evolved from *G. fornicata* Plummer in the Lower *Belemnitella mucronata* Zone. Consequently, the earliest forms of *G. rugosa* are quite similar to *G. fornicata*. Typical specimens of *G. rugosa*, however, differ from *G. fornicata* in: (1) being ventrally more convex, (2) having an early rugose surface, (3) usually having more broadly spaced keels without the distinctive 'cone in cone' arrangement of *G. fornicata*, and (4) having chambers less strongly curved. *G. rugosa* somewhat resembles *G. linneiana tricarinata* (Quereau) but is more convex dorsally, and the dorsal surface of the early chambers is rugose compared to the finely hispid chamber surface of *G. linneiana tricarinata*. Dr. Pierre Marie has kindly compared specimens of *G. rugosa* from Culver Cliff with the holotype of *G. rugosa* and has confirmed the identification of this species.

Occurrence. In the studied samples *G. rugosa* is restricted to the *Belemnitella mucronata* Zone and is most abundant in the uppermost sample, no. C10. Marie's type for *G. rugosa* is from the *Belemnitella mucronata* Zone of the Paris Basin.

Globotruncana cf. *ventricosa* White

Plate 71, figs. 2a-c

Cf. *Globotruncana canaliculata* var. *ventricosa* White 1928, p. 284, pl. 38, figs. 5a-c.

Cf. *Globotruncana ventricosa* White, Bolli 1957, p. 57, pl. 13, figs. 4a-c.

Description. Test free, very low trochospiral, dorsal side flat to slightly convex, ventral side strongly convex, evolute, umbilicate, about $2\frac{1}{2}$ whorls, equatorial periphery circular, weakly lobulate with 2 well-developed, closely spaced, beaded keels; dorsal keel diverges on to spiral side of test as dorsal sutural ridge; ventral keel diverges to umbilical side of terminal chamber face usually not coinciding precisely with ventral suture and usually not completely visible on ventral side of test, ventral keel then extends back along umbilical margin as a slightly raised ridge; chambers angular, ventrally inflated, 5 to $5\frac{1}{2}$ chambers in final whorl somewhat irregularly increasing in size; dorsal sutures distinct, oblique, strongly curved, raised, beaded; ventral sutures distinct, nearly radial, slightly curved, depressed; umbilicus moderately broad, deep, covered by a complex tegillum with marginal accessory apertures; primary aperture interiomarginal, umbilical; wall calcareous; wall structure not examined in thin section; chamber surfaces coarsely hispid becoming less hispid with growth; all of limited number of specimens coiled dextrally; average maximum diameter 0.58 mm.

Remarks. See remarks under *Globotruncana concavata* (Brotzen). The limited number of forms referred to *Globotruncana* cf. *ventricosa* from the Isle of Wight have more broadly curved chambers than the holotype of *G. ventricosa* and only 5 chambers in the final whorl instead of the usual 6 or 7. These forms, however, appear quite similar to Bolli's (1957, pl. 13, figs. 4a-c) excellent illustrations of *G. ventricosa*, although his specimens have smooth chamber surfaces compared to the hispid surfaces of the specimens from the Isle of Wight.

These forms are also similar to *Globotruncana bollii* Gandolfi. The keels on the specimens from the Isle of Wight are much more strongly developed and wider spaced, however, than those of *G. bollii*.

Occurrence. This species is very rare in the studied samples and was found only in samples C22 and C27 from the *Actinocamax quadratus* Zone (s.l.). Bolli (op. cit., p. 57) states that *G. ventricosa* appears to be restricted to the Upper Santonian and Campanian.

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NEW INFORMATION ON THE FORAMINIFERAL GENUS *PFENDERINA*

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ABSTRACT. *Pfenderina neocomiensis* (Pfender 1938) is redescribed from loose specimens for the first time and a new species, *P. trochoidea*, is described. *Kurnubia palastiniensis* Henson 1948, *Valvulinella wellingsi* Henson 1948, and *Valvulinella jurassica* Henson 1948, are united in the genus *Kurnubia* Henson 1948. *Kurnubia*, *Pfenderina* Henson, and *Meyendorffina* Arouze and Bizon 1958, are placed in the new family Pfenderinidae of the superfamily Lituolidea. This family is distinguished from the family Verneuilinidae, subfamily Ataxophragmiinae, by the numerous chambers per whorl, finely cribrate aperture and details of internal structure and from the family Orbitolinidae by the finer texture of the endoskeleton, the lesser development of the uniserial stage as compared to the spiral stage and details of the internal structure.

P. neocomiensis occurs in Europe only in the Valanginian and Berriasian, but in the Middle East it is typically found only from the Bathonian to the Argovian. The differing distribution in the two areas is so far without satisfactory explanation.

DUE to the discovery in beds of soft limestone of numerous well-preserved and separable specimens of *Pfenderina neocomiensis* (Pfender 1938) and a new species, *P. trochoidea*, we are able to describe *Pfenderina* fully for the first time. This form has previously been found only in hard limestones.

Comparing these two species with other Foraminifera, four other species show close similarities. These are *Kurnubia palastiniensis* Henson 1948, *Valvulinella wellingsi* Henson 1948, *V. jurassica* Henson 1948, and *Meyendorffina bathonica* Arouze and Bizon 1958.

While placing two of the above Jurassic species in the Carboniferous genus *Valvulinella* Schubert 1907, Henson remarked that ‘. . . certain details may require classification (of *V. wellingsi*) as a new genus when more is known of its ancestry’. Now that the structure of *Pfenderina* is much more fully known, the taxonomic position of the Jurassic species previously assigned to *Valvulinella* becomes apparent. As will be seen, these species do not belong to that genus, but may be assigned to the genus *Kurnubia* Henson 1948. Further, it arises that the genus *Kurnubia* is no longer to be assigned to the family Trochamminidae. *Pfenderina* has elsewhere rightly been linked with *Kurnubia* and the Jurassic ‘*Valvulinella*’ spp. Sigal (1952), although retaining Henson’s classification, drew parallels between these genera and both the family Orbitolinidae and the family Verneuilinidae, subfamily Ataxophragmiinae. Arouze and Bizon (1958) placed *Meyendorffina* in the Orbitolinidae. We consider that *Pfenderina*, *Kurnubia*, and *Meyendorffina* form a very close group, both morphologically and stratigraphically, that is sufficiently distinct from the families Verneuilinidae and Orbitolinidae to be recognized as yet another family, although it is related to both.

The Pfenderinidae are confined to one sedimentary facies group of clean, shallow-water limestones, but seldom occur in the shallowest sediments such as contain abundant oolites. In Europe derived limestone fragments have been described in association with occurrences of *Pfenderina*. Murat and Scolari (1956) described the facies in which *Pfenderina* occurs as ‘recifal’. However, there is no indication of biohermal or biostromal

origin of the beds in which Pfenderinidae occur, either in Europe or the Middle East. The Pfenderinidae are usually most abundant in limestones originally of fine grain. In such of these limestones as are little altered, few individual crystals can be clearly resolved at a magnification of $\times 40$ linear. The shell material in such cases, although mostly darker than the rock matrix, is of similar grain, but a more transparent epidermal 'vitreous' layer has been observed in some species. In our specimens there has often been growth of small rhombic crystals, probably of dolomite, indifferently in the matrix and in the shell material. These crystals are most conspicuous when formed in the darker shell material of a test. In all recorded occurrences, whether in a hard or soft limestone, the Pfenderinidae have been diagenetically affected to some extent and all published figures are to some extent obscure because of it. Ours are not free from this defect, but it is marked in Pfender's original figures of *P. neocomiensis*; Pfender (1938) referred to the 'aspect guilloché' of the chamber walls. In some parts of the chamber wall this appearance is entirely due to the secondary growth of crystals, but a similar appearance is also caused by the perforations of the apertural part of the septa and by the labyrinthic passages in the endoskeleton of the central part of the chamber (see below). The original nature of the shell material is therefore often difficult to determine, but we believe that in the best of our own specimens the original microgranular texture has been comparatively little altered, and the fine texture in these cases is similar to that of many other Lituolidea. It is difficult to be sure that there were never any agglutinated grains in the test, but it is most likely that all seeming inclusions are the result of secondary recrystallization.

In Europe *Pfenderina* has been recorded from France and Switzerland in beds of Berriasian and Valanginian age but never from the Jurassic. In the Middle East *Pfenderina* is recorded from the Bathonian to the Argovian (Oxfordian) with its greatest abundance in the Bathonian and Callovian. Records of younger age are suspect and even if any are eventually substantiated, they relate to rare occurrences. In both southern Europe and the Middle East there are both Upper Jurassic and Neocomian limestones indicative of an environment suitable for *Pfenderina*. It has been thought that both areas, lay in the same faunal province and in the same major depositional basin. We can detect no significant difference between the specimens of *P. neocomiensis* from the two areas, and from published information it seems most unlikely that any substantial error has been made in dating any of the relevant beds in either region. The peculiarly varying distribution of *P. neocomiensis* therefore presents a problem.

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The figured specimens have been deposited in the British Museum (Natural History). The relevant registration numbers are given in the plate explanations.

FAMILY PFENDERINIDAE NOV.

Diagnosis. The shell material is microgranular, without detectable agglutinated material. The early chambers are always spirally arranged and many per whorl. The chamber arrangement sometimes produces a low trochospire throughout. Occasionally the test is almost or quite planispiral, but more often the arrangement tends to become helico-

spiral. The later chambers may be uniserially arranged. The chambers are low; in low trochospiral tests they are unequally equitant; in helicospiral tests they are nearly oval and each occupies most of the area of the base; when uniserially arranged they are circular and slightly dished. The apertural face has a large, finely perforate, central area which constitutes a cribrate aperture. The peripheral part of the apertural face is imperforate and corresponds to an outer zone of the chamber which may be empty or have a partial subdivision into subepidermal cells. The part of the chamber behind the apertural area is filled with endoskeleton, originally labyrinthine but sometimes remaining so in the later chambers only. A secondary intercameral foramen is present in the form of a slit or circular aperture near the margin of the infilled part of the chamber. No corresponding external aperture has been observed. In helicospiral and uniserial developments the infilled parts of the chambers aggregate to form a columella. In low trochoid tests the columella cannot form but there is a homologous spiral structure.

Affinities with other families. Henson (1948) classified these foraminifera in the Family Trochamminidae, but this was a formal decision taken to avoid disturbance of the existing classification of *Valvulinella* Schubert 1907 and he recognized that this was possibly a temporary expedient. In this paper we take the general outline of the family classification from Sigal (1952) who, although he retained Henson's classification formally, indicated parallels between the genera now ascribed to the Pfenderinidae and those of both the Orbitolinidae and the Verneuilinidae, especially of the subfamily Ataxophragmiinae. The members of both these families typically have agglutinated shell material and therefore appear very different from the Pfenderinidae. However, in both families there are species of the type genus which lack agglutinated grains. The Verneuilinidae are typically strongly trochospiral, tend to reduce the number of chambers per whorl and usually have a single aperture. In species with a cribrate aperture, it is usually possible to trace its derivation from a single one. The Pfenderinidae have many chambers per whorl, never two or three, although they may have a uniserial terminal stage. The apertural pores are fine and numerous. The chambers are low, while those of the Verneuilinidae tend to be high and globose. The two families contain certain morphologically similar genera, but the various differences of internal and external organization indicate that the resemblances are due to homoeomorphic developments arising in distinct stocks. The fine texture of the central zone of the chamber is distinctive of the Pfenderinidae. The genera of the Orbitolinidae also have resemblances to the Pfenderinidae which cannot be lightly dismissed. If it were considered that the separation of the family Pfenderinidae was not justifiable, we should place these foraminifera in the Orbitolinidae. These two groups have certain features in common. Where subepidermal partitions are present, the nature of these is very similar. In both families the typical aperture is cribrate with numerous fine pores. The part of the chamber behind this porous area is occupied by endoskeleton that is penetrated by labyrinthine passages in *Orbitolina* and in the Pfenderinidae. But those of the Pfenderinidae are finer and may become secondarily infilled. The more typical Pfenderinidae have the trochoid development of the spire to distinguish them from the Orbitolinidae; *Orbitolina* itself has a plane initial spire in the microspheric form (although some textbooks state otherwise; Douglas 1960) and a helicoid spire is not usual until Tertiary species such as *Dictyoconus indicus* appear. But the variation from trochospiral towards

planispiral seen in *Pfenderina trochoidea* and the near planispiral arrangement in *Meyendorffina* prevent us from using the manner of coiling of the spire as a diagnostic character. The dominance of the uniserial stage over the spiral stage and the habit of rapid increase of chamber diameter in the Orbitolinidae also distinguish them from the Pfenderinidae, but this, too, cannot be taken to be a truly diagnostic character, for some species of the Pfenderinidae do show a well-developed uniserial termination. The Pfenderinidae have intercameral foramina which, together with spiral grooves or open spaces connecting them, form very characteristic structures not observed in the Orbitolinidae. This is certainly one of the more striking differences between the members of the two families, but it cannot be concluded from this feature alone that they are far apart genetically.

In brief, the creation of the new family Pfenderinidae is suggested because the species concerned have so many features in common as to indicate that they belong to one restricted branch of descent. At the same time it is suspected that this branch is not far removed from others, especially that of the Orbitolinidae. It so happens that known Pfenderinidae have such stratigraphic distribution as to support the idea that they are a natural group. One anticipates difficulty in determining lines of descent from ancestral species in which differentiation between the Pfenderinidae, Orbitolinidae, and Verneuiliidae was incomplete.

Distribution. The Pfenderinidae are known from the Bathonian to the Valanginian. They have been reported from Europe, North Africa, and the Middle East. They occur only in shallow-water limestones.

Genus PFENDERINA Henson 1948 (1947)

Type species. *Eorupertia neoconiensis* Pfender 1938.

Description. The shell material, as seen in fossil specimens, appears microgranular and dark in thin section, excepting sometimes for a thin epidermal layer of 'vitreous' appearance. It is believed that these appearances reflect very nearly the true nature of the original shell substance and that there was never any agglutinated material. Small calcite and dolomite rhombs commonly observed within specimens are believed to be of diagenetic origin. Except for apertural pores the chamber wall is imperforate.

The test is spiral, varying from strongly helicoid to almost planispiral. In the known species almost equal numbers of individuals are dextral and sinistral. There are numerous chambers per whorl. Typically the chambers are low and rather oval, each occupying a considerable part of the base and overlapping the axis of coiling. An outer, crescentic part of the chamber is empty and the part of the septum covering this is imperforate. The large remaining inner part of the chamber is occupied by endoskeleton in which there are labyrinthine passages and the corresponding part of the septum is perforated by the pores of the cribrate apertures. Where the chambers are appropriately arranged, in a high trochoid or helicoid spire, the aggregation of the infilled parts of the chambers forms an axial columella. In the variants tending most towards being planispiral the chambers are unequally equitant and cannot form a straight columella. A homologous spiral structure is then formed. In the earlier chambers of the test the labyrinthine passages were infilled during the life of the organism and the columella or

homologous spiral structure is solid in this part. A secondary intercameral foramen is present in each septum in the form of a circular aperture. These foramina lie in what amounts to a spiral groove in the margin of the columella. No corresponding external aperture has been seen.

Affinities with other genera. Arising from our studies of *Pfenderina* and many specimens from various localities of the Jurassic species of *Valvulinella*, we see no real objection to placing the Jurassic species which were tentatively assigned to *Valvulinella* by Henson (1948) in the genus *Kurnubia* Henson 1948. As was recognized by Henson, the link is very weak between the Jurassic species, *Valvulinella jurassica* and *V. wellingsi*, and *Valvulina youngi* Brady 1876, the Carboniferous type species of *Valvulinella* Schubert 1907, for the latter lacks a columella. *V. jurassica* and *V. wellingsi* could, in our opinion, very well be transferred to *Kurnubia*. It might be objected that this involved including in one genus species with and without a terminal uniserial stage. However, the three species, so highly specialized in some respects, are at present shown to differ only in minor details of chamber shape and arrangement, according to which there may or may not result the development of a uniserial termination. For this reason we would include the three species in the same genus at this time, though we would note that further studies of really good specimens of the type species, *K. palastiniensis*, might eventually reveal features which would justify the distinction of two genera.

Accepting the above, the diagnostic distinction between *Kurnubia* and *Pfenderina* is the lack of subepidermal partitions in the latter. There are other distinctive features. In all known species the columella is proportionally smaller in *Kurnubia* than in *Pfenderina*. It seems that *Pfenderina* was the ancestor of *Kurnubia* and that decrease in the size of the columella was an evolutionary trend which accompanied the development of subepidermal partitions. In *Kurnubia* there appears to have been little or no secondary infilling of the labyrinthine passages of the columella. In *Kurnubia* the secondary foramina lie just outside the columella whereas in *Pfenderina* they are aligned with spirally arranged depressions in the margin of the columella. There can be no doubt, however, that the genera are closely related.

Meyendorffina has all the characteristics of the Pfenderinidae in chamber structure and general appearance, but is planispiral, or nearly so. In this it contrasts with the more typical, elongate-trochospiral Pfenderinidae, but does not differ markedly from the more planispiral variants of *Pfenderina*. It is terminally uniserial, as is the case with one species of *Kurnubia*. Arouze and Bizon (1958) placed *Kilianina* in the family Orbitolinidae, in association with *Meyendorffina*. Its structure of chambers about an open umbilical space is not comparable either in the Orbitolinidae or the Pfenderinidae. We would place this genus provisionally in the family Trochamminidae, subfamily Tetra-taxinae.

Distribution. *Pfenderina* has been recorded from the Bathonian to the Valanginian.

Pfenderina neocomiensis (Pfender)

Plate 73, figs. 1-9; Plate 74, figs. 1-3; Plate 75, fig. 1; Text-fig. 1, A-D.

Eorupertia neocomiensis Pfender 1938.

Pfenderina neocomiensis (Pfender); Henson 1948 (1947).

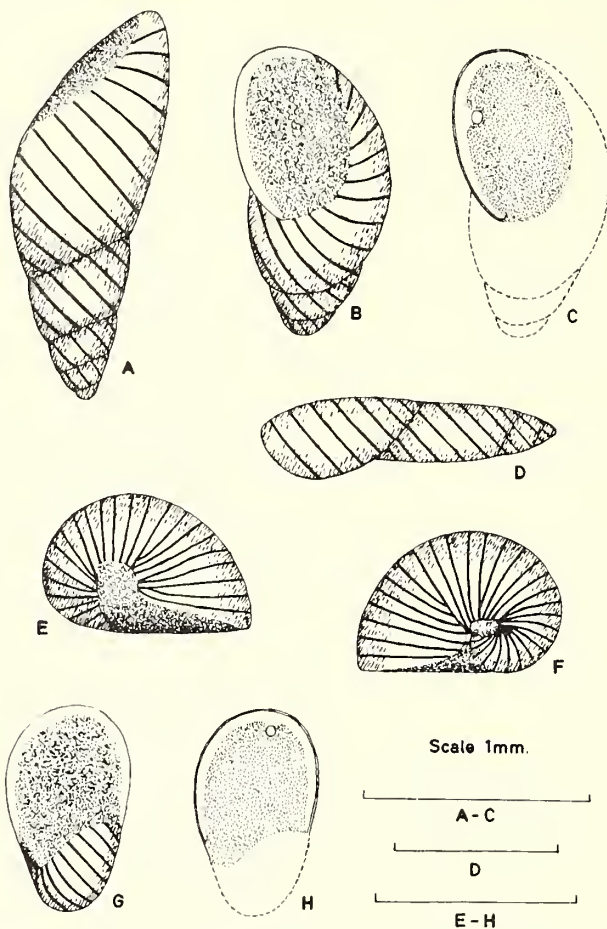
Pfenderina neocomiensis (Pfender); Murat and Scolari 1956.

Pfenderina neocomiensis (Pfender); Marie and Mongin 1957.

Pfenderina neocomiensis (Pfender); Hudson 1958.

Pfenderina neocomiensis (Pfender); Hudson and Chatton 1959.

Material. One hundred and twenty-six separate specimens and twenty thin sections from samples from deep bore-holes on the Qatar Peninsula of Arabia and bore-hole Najmah No. 29, Iraq. Figured specimens: P. 43713, 43719–25, 44639–40.



TEXT-FIG. 1. A–D, *Pfenderina neocomiensis* (Pfender). A–B, Two external views of the same specimen. C, Reconstruction corresponding to B of the relationship of the crescentic chamber space, endoskeleton and foramen in the last chamber. Labyrinthic passages not shown. D, External view of another specimen. E–H, *Pfenderina trochoidea* sp. nov. E–G, Ventral, dorsal, and apertural views of the same specimen. H, Reconstruction corresponding to G of interior of last chamber.

Description. The test rarely exceeds 2 mm. length, usually being about 1.5 mm. The width varies from 0.5 to 1.0 mm. The apex is usually acutely conical but in some specimens is more rounded. In all cases the angle of the spire decreases in later whorls. The last two whorls may show negligible increase in diameter. The adult test usually has 4 to 5 whorls

with 14 or more chambers in the last whorl, the greatest number seen being 20. Features of dimorphism have not yet been detected. The spiral suture lies in a groove and the septal sutures are very weakly indented. The septal sutures are at right angles to the spiral suture and in later whorls both are at about 45° to the axis of coiling. The septal spacing is about 0.1 mm. and the whorl height, measured in the direction of the axis, is about 0.6 to 0.8 mm. in the fourth whorl. The part of the chamber wall exposed between septal sutures is imperforate. The apertural face is roughly oval and slightly convex. There is an outer imperforate rim over the crescentic space within the chamber and the rest of the apertural face is finely perforate. The chambers all overlap the ventral pole of the axis of coiling and each therefore occupies most of the base, which is very obliquely set to the axis. Each chamber has an outer crescentic space without internal structures, but the central zone behind the apertural area is infilled with endoskeleton, the material of which has the same appearance as, and is continuous with, the material of the adjoining chamber wall. In the last two or three chambers, and sometimes in a few earlier chambers, labyrinthine passages can be seen within the endoskeletal material, but in the earliest chambers these passages become secondarily filled with material that has the same optical properties as the remainder of the endoskeleton. The endoskeletal material thus becomes aggregated into a columella that appears quite solid. In each septum there is a round intercameral foramen, placed at a point about equidistant from the ends of the crescentic chamber spaces. The foramina lie in line with notches in the outer margin of the endoskeletal material and these notches together give the appearance of a spiral groove around the outside of the columella. The foramina seem to have been formed secondarily because no trace of a similar aperture has been seen on the apertural face. The appearance of the intercameral foramina in a decorticated specimen recalls that of the tunnel in the Fusulinidae, but the resemblance is, as far as we can tell, fortuitous.

Remarks. Our specimens, on the average, seem to show less inflation of the chamber walls and more infilling of the labyrinthine passages than Pfender's original specimens, but the differences are too slight to be regarded as significant.

Distribution. Europe. Known from the Berriasian–Valanginian 'marbre bâtard' of southern France and western Switzerland. Pfender described *P. neocomiensis* from the Valanginian of Provence. Murat and Scolari (1956) gave a careful summary of occurrences in France and Switzerland known to that date and Dufaure (1958) gave further records from France. All agree in dating the occurrences as Berriasian or Valanginian and investigations on the Upper and Middle Jurassic of that area are adequate to create the strong presumption that the species is absent from pre-Neocomian beds in Europe.

Middle East. Known from the Shuqra formation (Oxfordian) of south-west Arabia; the *Shuqraia* beds (Oxfordian) of Kurnub, Palestine; the upper part (Callovian to Oxfordian) of the Lower Musandam Limestone of Jebel Hagab, Oman; the Uwainat member and lower parts of the Araej formation (Bathonian) of Qatar; the Najmah formation (Callovian–Oxfordian) of Iraq. The ages cited are taken from Hudson (1954), Hudson (1958), Hudson and Chatton (1959), and Dunnington (1960). The evidence for the dating of the Araej formation will appear shortly (Sugden, in press). Hudson and Chatton (1959) recorded Jurassic occurrences as *Pfenderina* sp. because at the time that their publication was prepared *P. neocomiensis* and *P. trochoidea* had not been differentiated. *Pfenderina* is also reported from the Muhawir formation (Bathonian) of

north-west Iraq (Dunnington 1960) where *P. neocomiensis* is probably present, but the specimens are too poor for certain specific identification.

Doubtful records exist of *Pfenderina* in the Riyadh group (Kimeridgian) and Thamama group (Valanginian) of Qatar (Hudson and Chatton 1959) and from the Cenomanian of Jebel Abd el Aziz, Syria (Henson 1948). On these reported occurrences we would comment that the records need verification. If any are indeed true they refer to very rare occurrences and we would note that when dealing with rare and poorly preserved material it is easily possible to confuse *Pfenderina* with various other superficially similar genera.

Pfenderina trochoidea sp. nov.

Plate 73, figs. 1–7; Plate 74, figs. 3–6; Plate 75, figs. 1–3; Text-fig. 1, E–H.

Holotype. P. 43728. Figured specimens: P. 42967, 43710–16, 43726–31, 44641.

Type locality. The Uwainat member of the Araej formation in deep bore-holes of Jebel Dukhan, Qatar Peninsula of Arabia. Additional locality: lower part of the Najmah formation in deep bore-hole Najmah 29, Iraq.

Material. One hundred and thirty-one separate specimens and eight thin sections.

Description. The test rarely exceeds 1 mm. in axial length; the maximum diameter may attain 1.5 mm. and often exceeds 1 mm. while the smaller diameter, at right angles to this, is usually smaller than 1 mm. The spire is typically low trochoid with slight dorsal overlap but strong ventral involution. However, in some specimens the spire is almost plane and in such cases the chambers are unequally equitant. Though the spire varies somewhat in its arrangement, no specimens have been found showing a trochoid spiral sufficiently elongate to be interpreted as intermediate to *P. neocomiensis*. With the possible exception of the nucleoconch, *P. trochoidea* is identical with *P. neocomiensis* in all characters which do not depend on the shape of the spire and its measurements. The nucleoconch is roughly oval, measuring about 0.15×0.1 mm. A median constriction probably indicates a former partition between the proloculus and deuterococonch. The

EXPLANATION OF PLATE 73

Figs. 1–7. *Pfenderina neocomiensis* (Pfender) 1938; P. 43719–25; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, $\times 20$. These separated specimens are mostly decorticated to a varying extent. Figs. 2, 3, and 6 show the serried septa with a large foramen in each, causing the appearance of a 'tunnel'. Fig. 3 is the most entire specimen and shows the apertural face. The slightly rugose appearance of this, not clearly seen in the photograph, is an indication of the numerous fine pores forming the cribrate aperture of the columella region. There is no aperture corresponding to the large foramen of each septum.

Figs. 8–15. *Pfenderina trochoidea* sp. nov.; P. 43726–32, 42967; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, $\times 20$. These picked specimens were found with those illustrated in figs. 1–7.

The same general features can be seen, the best view of the apertural face being given by fig. 13.

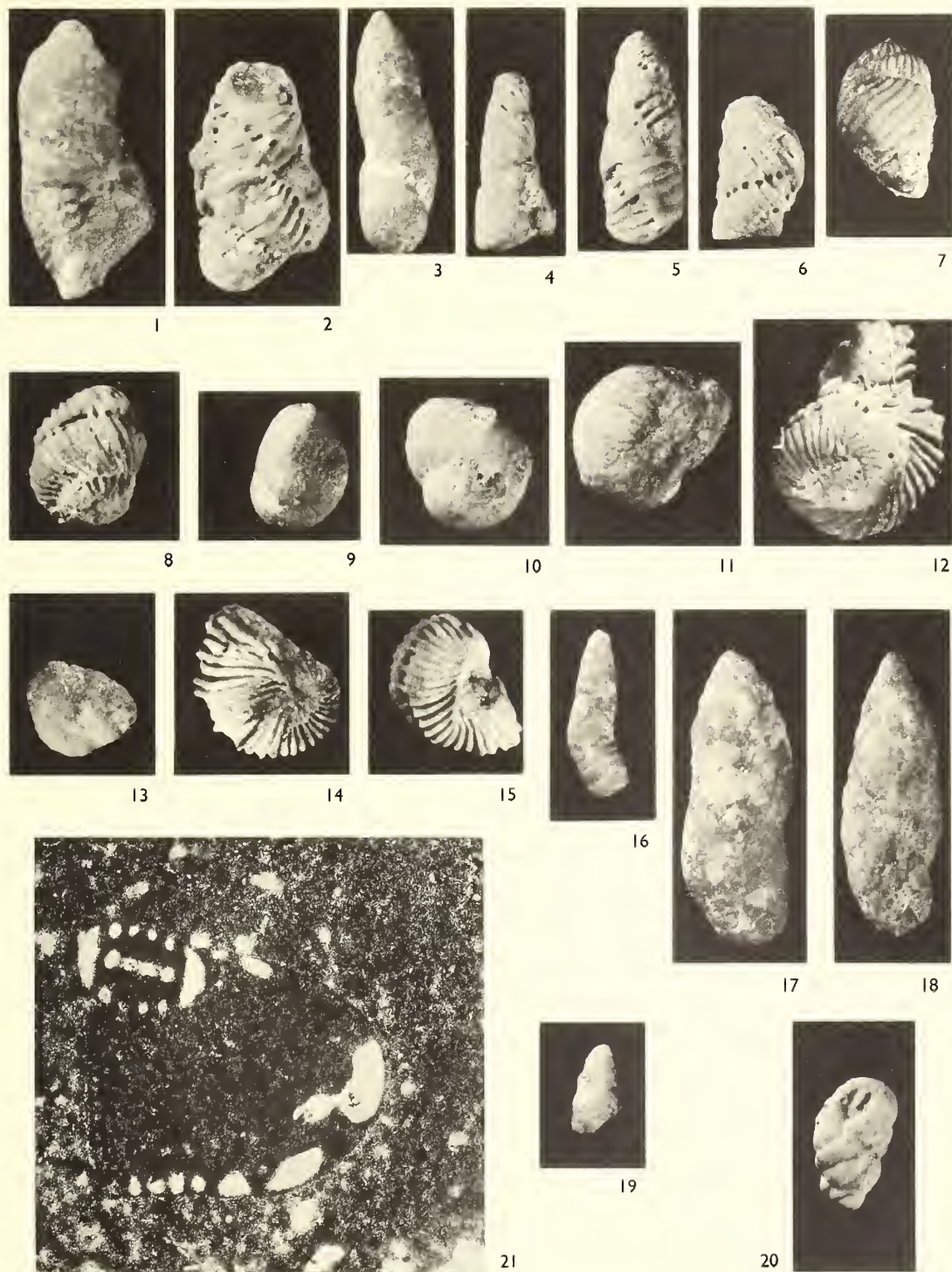
Fig. 16. *Kurnubia palastiniensis* Henson 1948; P. 42968; topotype specimen, $\times 20$.

Figs. 17–18. *Kurnubia wellingsi* (Henson) 1948; P. 42969–70; topotype specimens, $\times 20$.

Fig. 19. *Kurnubia jurassica* (Henson) 1948; P. 44637; topotype specimen, $\times 20$.

Fig. 20. *Arenobulimina*? sp.; P. 44638; Lower Cretaceous Thamama Group, Qatar Peninsula of Arabia, $\times 20$. This specimen is illustrative of specimens that could be confused with *Pfenderina* or *Kurnubia*. Note the single, toothed, aperture and the absence of any area that could form a columella.

Fig. 21. *Pfenderina trochoidea* sp. nov.; P. 43716; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, $\times 55$.



chambers of the more trochoid specimens are similar to those of *P. neocomiensis*, being low, more or less oval, and possessing a narrow outer empty space and an internal part infilled with labyrinthine endoskeleton. The cribrate apertures and secondarily formed intercameral foramina are the same as those of *P. neocomiensis* but the infilling of the labyrinthic passages progressed more slowly, so that in section they are seen in about eight of the later chambers or even more. The shape of the apertural face is modified to a distorted horseshoe shape in the more planispiral specimens and the chambers tend to lose their overlap of the ventral pole of the axis of coiling. The infilling of the chambers therefore takes the form of a spiral, not that of a columella.

Remarks. *P. trochoidea* is so similar to *P. neocomiensis* in all characters not affected by the helicoid component of the coiling, that it is surprising that no intermediate specimens have been found. It is unlikely that the two species represent alternate generations of one population, because *P. neocomiensis* is found alone in rocks of later age. The ecological requirements of the two species seem to have been identical, and closely similar to those of *Kurnubia* spp.

Sixty-one separate specimens were found to be dextrally coiled and seventy sinistrally coiled. The ratio is not considered to differ significantly from 1:1.

Distribution. This species has been recorded only from the Middle East, in the Bathonian Uwainat member of the Araej formation, and in the Oxfordian–Callovian Najmah formation. In both cases it occurs with *P. neocomiensis* but wholly below all occurrences of *Kurnubia* spp. Records of *Pfenderina* sp. in the Bathonian Muhaiwir formation of Iraq and in groups *e* and *f* of the Lower Musandam Limestone of Jebel Hagab, Oman, which are also dated as Bathonian, may include this species.

Genus KURNUBIA Henson 1948 (1947) emended

Plate 73, figs. 16–19; Plate 76, figs. 1–8

Type species. *Kurnubia palastiniensis* Henson 1948 (1947).

Emended diagnosis. The test is trochoid to strongly helicoid in known species, sometimes with a uniserial termination developing ventrally along the axis of coiling. The chambers are low and oval in shape in the spiral stage, each occupying most of the base. Each has a cellular subepidermal layer opening into a narrow empty space, inside which is a central labyrinthine zone. The overlap of the chambers over the ventral axis causes the labyrinthine parts of the chambers to aggregate to form a columella. In the uniserial stage the chambers are circular, but otherwise similar to those of the spiral stage. The aperture is cribrate, with small pores, and overlies and connects with that part of the chamber which is infilled with labyrinthine endoskeleton. This area tends to be proportionally larger in uniserial chambers than in spiral ones. There is usually little or no secondary infilling of the labyrinthine passages of the earlier chambers. Sections show what appear to be secondary intercameral foramina against the columella but the complexity of the structure makes them difficult to distinguish with certainty and their presence needs to be confirmed by observation on good solid specimens.

Remarks. The shell material was probably originally microgranular and imperforate

but known specimens are all diagenetically altered, so that it is difficult to assess the original nature of the shell material. There are no included agglutinated grains.

Kurnubia, as here redefined, includes the Jurassic species *Valvulinella wellingsi* and *Valvulinella jurassica*, both described by Henson (1948). In view of Henson's remarks on the close relationship of *K. palastiniensis* to *V. jurassica*, with which we agree, it seems undesirable to separate these species generically, particularly as only three trivial names are involved.

Kurnubia, as here redefined, differs essentially from *Pfenderina* in possessing subepidermal cells in the chambers. Also, in *Pfenderina* there is a strong tendency to infilling of the labyrinthine zones of the chambers. This is apt to disguise their essential similarity at formation to those of *Kurnubia*. Despite important internal differences some species of the two genera are superficially similar.

We do not propose to redescribe species of *Kurnubia* but specimens have been figured for comparison with *Pfenderina*. We have seen specimens that seem to be intermediate between *K. wellingsi* and *K. jurassica* but these require further study.

Distribution. Oxfordian to Valanginian of south Europe, North Africa, and the Middle East.

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EXPLANATION OF PLATE 74

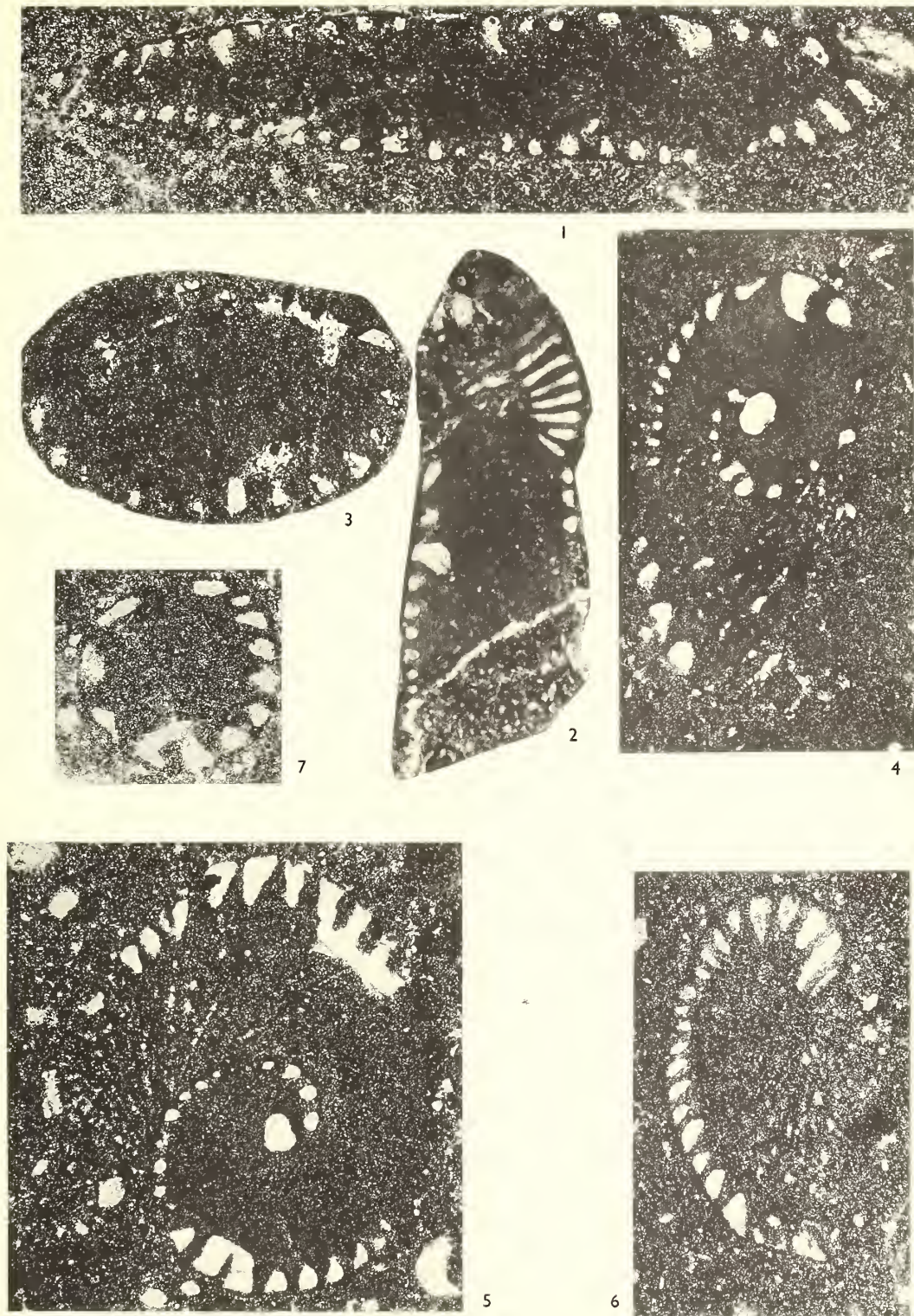
- Figs. 1-3, 7. *Pfenderina neoconiensis* (Pfender) 1938; 1, 3, P. 44639; 2, P. 44640; 7, P. 43712; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, $\times 55$. Random sections. Fig. 2 shows the progressive obliteration of the cavities in the columella, which appears to be solid above the last six chambers. 7, Section normal to the axis of coiling.
 Figs. 4-6. *Pfenderina trochoidea* sp. nov.; 4, 5, P. 43710; 6, P. 43711; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, $\times 55$. 4, 5, Sections showing the complete spires of two almost planispiral specimens.

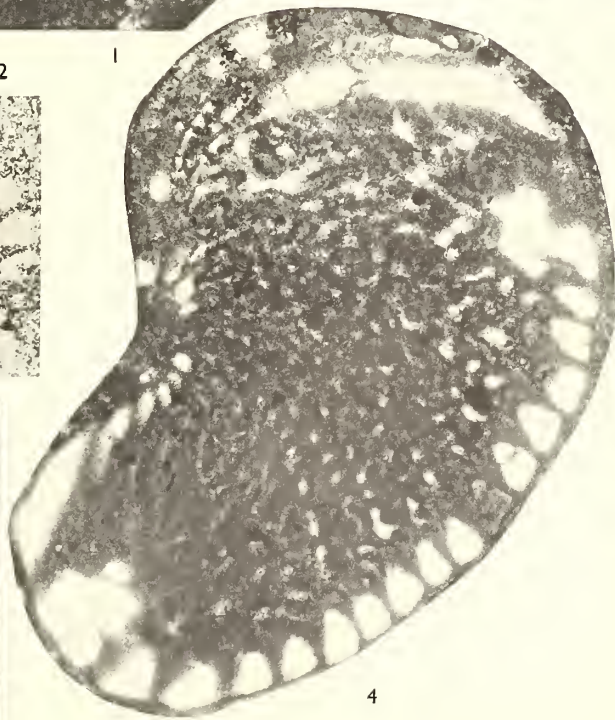
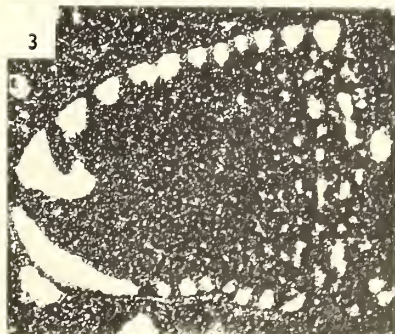
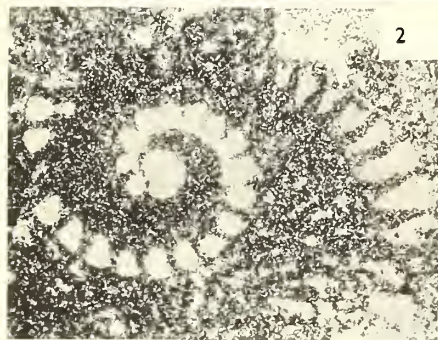
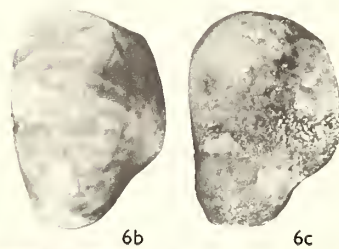
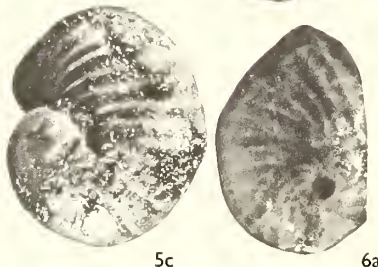
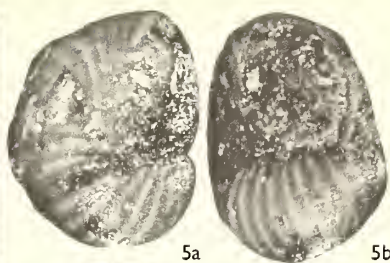
EXPLANATION OF PLATE 75

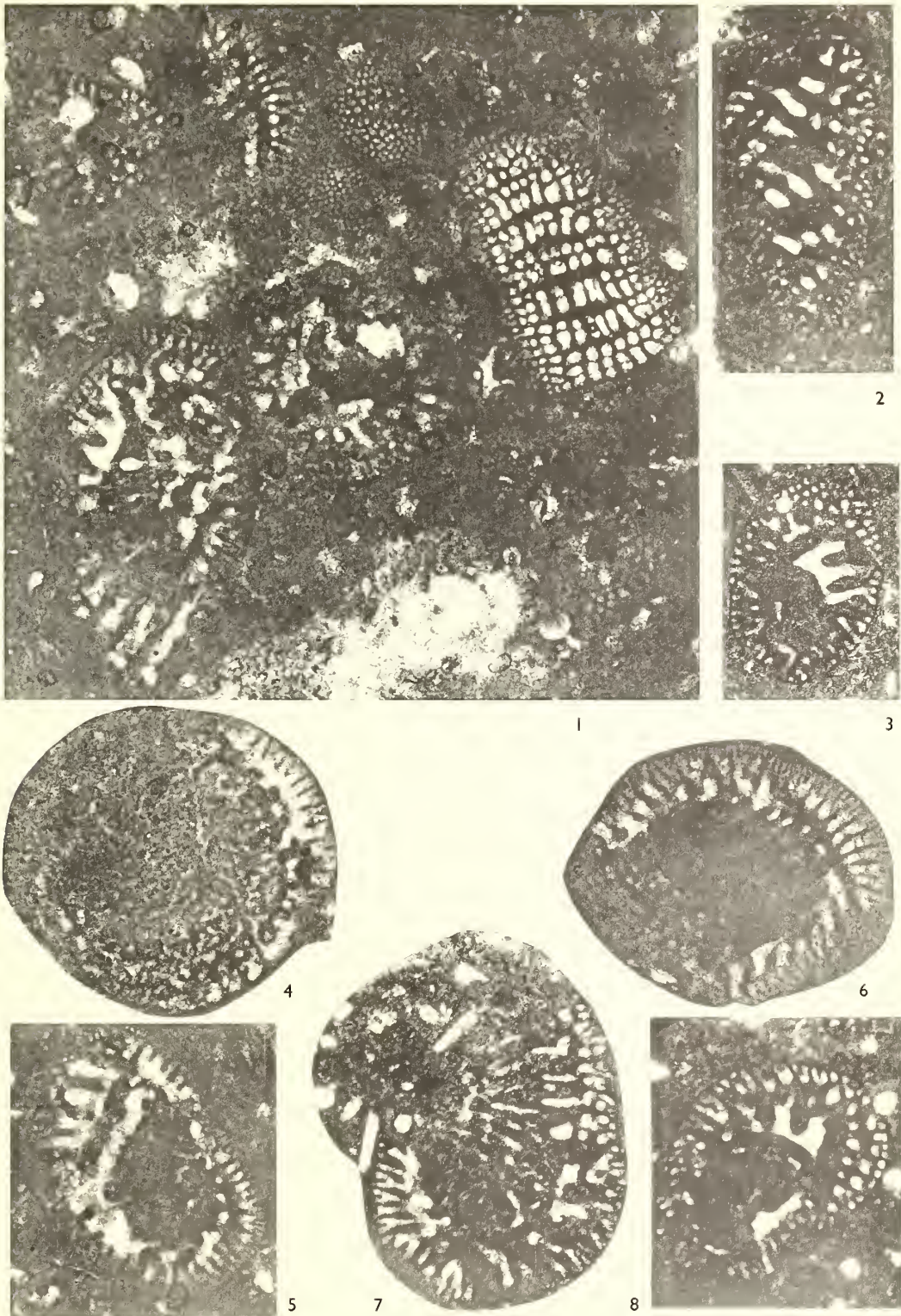
- Fig. 1. *Pfenderina neoconiensis* (Pfender) 1938, and *P. trochoidea* sp. nov.; P. 43713; Najmah limestone, Callovian, Najmah well no. 29, Iraq, $\times 55$.
 Figs. 2-4. *Pfenderina trochoidea* sp. nov.; 2, 3, P. 43714-5; 4, P. 44641; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, $\times 55$. Random sections.
 Figs. 5-6. *Pfenderina trochoidea* sp. nov.; 5a-c, P. 43728, holotype; 6a-c, P. 43727; Uwainat limestone, Bathonian, Qatar Peninsula of Arabia, $\times 20$. 6, Nearly planispiral specimen that nevertheless shows distinct asymmetry of the apertural face.

EXPLANATION OF PLATE 76

- Figs. 1-8. *Kurnubia wellingsi* (Henson) 1948; 1, 4, 5, P. 43717; upper part of the Najmah limestone, Oxfordian, Najmah well no. 29, Iraq. 2, 3, 6-8, P. 43718; Upper Jurassic limestone; Broumana, Syria. Random sections, $\times 55$. All the figures on this page are intended to show the similarity of structure between *Kurnubia* and *Pfenderina*; the only distinction being the subepidermal partitions.







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NEW GENERA AND SUBGENERA OF MESOZOIC BIVALVIA

by L. R. COX

ABSTRACT. The following new taxa, belonging to the families stated, are diagnosed and discussed: *Palmoxytoma* subgen. nov., type species, *Pecten cygnipes* Young & Bird, Middle Lias (Oxytomidae, now advanced from subfamily to family rank); *Rhaetavicula* gen. nov., type species, *Avicula contorta* Portlock, Rhaetic (Pteriidae ?); *Ornithopecten* gen. nov., type species, *Aviculopecten bosniae* Bittner, Middle Trias (Aviculopectinidae); *Ensio* gen. nov., type species, *Ptychomya agassizii* Lycett, Bajocian (Astartidae).

THE purpose of this paper is to establish new genera for certain Mesozoic bivalves, previous generic assignments of which appear unsatisfactory, and a new subgenus of *Oxytoma* for a small and distinctive group of species belonging to this genus. It is intended to use one of the new generic names in a handbook, *British Mesozoic Fossils*, shortly to be published by the British Museum (Natural History), and all four names in the volume of the *Treatise on Invertebrate Paleontology* which is to be devoted to the Bivalvia.

The Linnean name Bivalvia was the earliest term for the molluscan class which has since become known by the alternative names Lamellibranchia or Pelecypoda. Its use is now becoming increasingly widespread and it has been adopted in several of the leading modern works of reference, including J. Thiele's *Handbuch der systematischen Weichtierkunde* (Jena, 1929-35) and F. Haas's contribution on the class in question, forming Band 3, Abt. 3 (1929-35) of the modern edition of Bronn's *Klassen und Ordnungen des Tierreichs* (Leipzig). It is expected that it will be adopted in the appropriate volume of the *Treatise*.

Acknowledgements. I must thank the authorities of the Geological Survey for the loan of the holotype and other specimens of *Ensio agassizii* together with a specimen of the little-known right valve of *Rhaetavicula contorta*. Dr. R. J. G. Savage, of Bristol University, has kindly lent three further specimens of this valve.

ERECTION OF A NEW FAMILY OXYTOMIDAE AND OF A NEW SUBGENUS

Until recently *Oxytoma*, *Meleagrinella*, *Maccoyella*, and related Mesozoic genera were included in the family Pteriidae, based on the living genus *Pteria* Scopoli, 1777 (synonym, *Avicula* Bruguière, 1791). Ichikawa (1958), however, has proposed that these genera should constitute a new subfamily Oxytominae, which he has included in the family Aviculopectinidae as extended by Newell (1938), and hence in the superfamily Pectinacea rather than in the Pteriacea. Their affinity with the Aviculopectinidae is suggested by the deep subauricular notch in the right valve and by the ornament of radial ribs and riblets which are commonly of two or three orders of strength. On the other hand, their inequilateral, prosocline form and the much reduced size of the right anterior auricle distinguish them from *Aviculopecten* itself, and Ichikawa has pointed out the important difference that the inner ostracum of the valves of their shell is calcitic, with a crossed-lamellar structure, and not aragonitic as in typical Aviculopectinidae, including *Pseudo-*

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monotis (cf. Newell 1938, p. 92). A further difference is that the pallial line, which has been observed in *Oxytoma*, *Meleagrinella*, *Maccoyella*, and *Pseudavicula*, is discontinuous and broken up into small pits (as in Recent Pteriidae), whereas in the Aviculopectinidae it is continuous.

It is now suggested that these differences are important enough to justify the elevation of the Oxytominae to family rank as Oxytomidae. It is considered that this family was descended from the Aviculopectinidae and should be included in the superfamily Pectinacea. Certain points of resemblance to the Pteriidae are, it is thought, attributable to parallel evolution. Members of the Oxytomidae are clearly distinguished from that family by the absence of an aragonitic, nacreous inner ostracum.

Genus OXYTOMA Meek 1864

The new taxon *Palmoxytoma*, proposed below, is considered to be a subgenus of *Oxytoma*, the type species of which, by original designation, is *Avicula muensteri* Goldfuss 1836. The generic characters of *Oxytoma* may be summarized as follows: shell suborbicular and acline to ovate or broadly lunate and prosocline; valves very unequal and commonly discordant, the left one of varying convexity with the umbo protruding, the right one flat or feebly convex; posterior wing of both valves more or less elongated, sharply pointed; left anterior wing small, obtuse; right anterior auricle small, subauricular notch deep, acute, with a ctenolium, an angular sinus of the shell margin extending on the inner side of the notch; ligamental area almost parallel with plane of commissure of valves in left valve, almost perpendicular to it in the right; no hinge teeth; left valve in most species ornamented with radial ribs or riblets.

Subgenus PALMOXYTOMA subgen. nov.

Subgeneric name. Latin *palma*, hand; *Oxytoma*, a genus of Bivalvia. Gender, feminine.

Type species. *Pecten cygnipes* Young & Bird (1822, p. 235, pl. 9, figs. 4, 6), Middle Lias.

Diagnosis. Large, orbicular, only slightly prosocline *Oxytoma*; left valve moderately to strongly convex, right valve almost flat; left valve with a small number (3 to about 8) of narrow, prominent, spinose ribs which give rise to projections or narrow digitations of the valve margin and are separated by broad, flat intervals which are smooth or bear fine radial striations; the ribs increasing by intercalation in some specimens; right valve with a small number of faint, narrow radial grooves and, in some specimens, fine radial striations; posterior adductor scar more nearly median than in *O. (Oxytoma)*.

Remarks. This subgenus, distinguished from *Oxytoma* s. str. by the large size and characteristic ornament of the shell, is confined to the Lias of Europe. The known species are *O. (Palmoxytoma) longicostata* (Stutchbury) (1839, p. 163, text-fig.), from the basal Lias (Pre-Planorbis Beds of the Hettangian) of the Bristol district, *O. (P.) magnifica* (Lundgren) (1881, p. 31, pl. 5, figs. 2-5), from the Hettangian of Sweden, and the type species, which occurs in the Middle Lias (Domerian) of England, France, and Switzerland. *O. (P.) cygnipes* has also been recorded from the uppermost Lower Lias (Lower Pliensbachian, Davoei Zone) of northern Germany, but specimens from this area have not been figured. The record (Jekelius 1915, p. 56, pl. 8, fig. 12) of its occurrence in the

uppermost Lower Lias of Romania was based on small, imperfect specimens which appear to have been wrongly identified.

ERECTION OF A NEW GENUS *RHAETAVICULA* (FAMILY PTERIIDAE?)

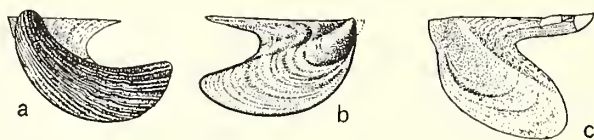
Genus *RHAETAVICULA* gen. nov.

Text-fig. 1

Generic name. From the geological stage name Rhaetic (derived from that of the Roman province Rhaetia or Raetia), and *avicula*, diminutive of the Latin *avis*, bird. Gender, feminine.

Type species. *Avicula contorta* Portlock (1843, p. 126, pl. 25A, fig. 16), Rhaetic.

Diagnosis. Small, narrow, lunate, strongly prosocline, highly inequivalve, valves probably discordant; left valve strongly convex, posteriorly upcurved, with a twisted



TEXT-FIG. 1. *Rhaetavicula contorta* (Portlock), Rhaetic. *a*, left valve (generalized), $\times 1.5$; *b*, right valve, borehole at Stowell Park, Northleach, Glos. (Geol. Surv. Mus. no. Bj 6116), $\times 1.5$; *c*, external impression of right valve, two small patches of shelly matter remaining on posterior wing, Emborough, Somerset (Bristol Univ. Coll. no. 549), $\times 3$.

appearance, its margins not in one plane; left umbo narrowly rounded, protruding, anteriorly placed; right valve almost flat, probably smaller than the left; posterior wing in both valves narrow, elongate, acutely pointed, with a deep rounded sinus below it; that of the left valve flattened and well demarcated from the body; left anterior wing small; right anterior auricle small, higher than long, not separated from body of valve by a notch; ligamental area narrow; body of left valve with narrow, unevenly spaced, rounded radial ribs, a few of their intervals with a secondary radial thread; posterior wing of left valve smooth; right valve smooth or almost so; an elongate posterior lateral tooth present in left valve, presence of an anterior tooth inconstant; muscle scars not observed.

Remarks. The type species is the most characteristic fossil of the Rhaetic stage of Europe and has also been found in Burma. The specimen from New Zealand recorded as *Pteria* cf. *contorta* by C. T. Trechmann (1923, *Quart. J. geol. Soc. Lond.* **79**, p. 273, pl. 12, fig. 10) is the internal mould of a small *Oxytoma*.

At many localities the bedding planes of Rhaetic rocks are strewn with specimens of its convex left valve, but specimens of the right valve are of very rare occurrence. The only published figures of this valve are those of Pflücker (1868, pl. 7, fig. 2) and Maud Healey (1908, pl. 5, figs. 4*a*, *b*). The first author depicts a broken specimen from Germany retaining part of this valve in place. It has a short, distally rounded anterior auricle with no notch below it. The specimen figured by Healey, also associated with the

left valve, was obviously also imperfect and her figure is not very clear. She describes the anterior auricle as 'very small and convex'. An isolated right valve, represented in her fig. 6 and identified as '*Pteria* sp. ind.', probably belonged to *R. contorta* also, but, if this was the case, the auricle, represented as sharply pointed, may have been inaccurately drawn.

Dr. R. J. G. Savage has sent me three right valves, from the black Rhaetic shales of Emborough, Somerset, which can be confidently assigned to *R. contorta*. All are impressions except for a little adherent shelly matter, and one, virtually an external mould, is illustrated in text-fig. 1c. The valve is without ornament. The anterior auricle, seen in all three specimens, is small and high in proportion to its length, with an outer angle of about 60°. No subauricular notch is present and there is only a slight concavity of the margin of the valve where the auricle joins the body.

I have not observed hinge teeth or their impressions in any British specimens of *R. contorta*, but this is probably due to their poor state of preservation. Pflücker (1868, p. 408) spoke of a clearly visible, lamelliform ('leistenförmig') lateral tooth on the posterior wing of the left valve and of a weak anterior tooth, the impression of which was visible in some specimens from Germany but not in others.

Originally described and for long widely known as *Avicula contorta*, this species is now generally cited as *Pteria contorta*, but it could not continue indefinitely to be known by this name, as by modern taxonomic standards it cannot be considered as congeneric with the living species *Pteria hirundo* (Linnaeus), type species of *Pteria*. The strong radial ribbing and the twisted form of the left valve are obvious distinctive characters. Beyrich (1862, p. 10) remarked that the Rhaetic species belonged to his newly founded taxon *Pseudomonotis*, but Pflücker (1868, p. 409) thought that it should be included in Beyrich's other genus *Cassianella*. This view was accepted by one or two authors of the next decade but was then abandoned and the original assignation to '*Avicula*' or *Pteria* adopted. There are points of resemblance between the Rhaetic shell and the more typical species of *Oxytoma*—the nature of the radial ornament, a tendency for this to be lacking on the right valve, and the flatness of the latter. In some specimens of *Oxytoma*, moreover (for example, the one figured as *O. muensteri* (Goldfuss) by Ichikawa, 1958, pl. 24, figs. 6a, b), the shell is pronouncedly lunate in shape and is distinctly reminiscent of the Rhaetic species.

It seems, however, undesirable at present to conclude that these resemblances indicate a close relationship between *Rhaetavicula* and *Oxytoma* and the consequent reference of the former genus to the Oxytomidae. All genera which I have accepted as members of that family agree in possessing a deep byssal notch below the right anterior auricle. Such a notch, as seen above, is absent in *Rhaetavicula*, the byssus having presumably passed through a slight gape of the valves. Consideration of various genera of the Pectinidae, it is true, shows that the presence of a deep byssal notch is not necessarily a feature of family significance. Should future work on the shell structure of *Rhaetavicula* (on which at present we have no certain information) lead to the conclusion that the inner ostracum of the valves was calcitic and not aragonitic and nacreous, this fact might be considered to outweigh the objection, based on the lack of a byssal notch, to the inclusion of *Rhaetavicula* in the Oxytomidae. For the present, however, it seems advisable to be conservative in referring this genus (perhaps with a query) to the family Pteriidae, based on the genus in which its type species has been usually placed.

ERECTION OF A NEW GENUS *ORNITHOPECTEN* (FAMILY
AVICULOPECTINIDAE)Genus *ORNITHOPECTEN* gen. nov.

Generic name. From Greek ὄρνις, bird; *Pecten*, genus of shells.

Type species. *Aviculopecten bosniae* Bittner (1903, p. 592, pl. 26, figs. 16, 17), Middle Trias.

Diagnosis. Small, acline to slightly prosocline, slightly inequivalve, but with the left umbo scarcely protruding; posterior wings pointed, more or less acute, not clearly demarcated from body of shell in most species; left anterior wing and right anterior auricle relatively small, subauricular sinus shallow to moderately deep; ornament of narrow, well-separated radial riblets, any increase of which in either valve is by intercalation, and of concentric lamellae.

Remarks. This new genus is proposed for the reception of a series of species of Triassic age which have so far been included in *Aviculopecten*. The characters of this genus have been fully discussed by Newell (1938, p. 43), who has shown that *A. planoradiatus* M'Coy must be accepted as its type species. *Ornithopecten* differs from *Aviculopecten* in the relatively small size of the left anterior wing and right anterior auricle (i.e. in the more inequilateral form of the shell), and in the nature of the ornament. In the right valve of *Aviculopecten* the radial ribs increase by bifurcation, whereas in *Ornithopecten* the increase (if any occurs) is by intercalation, as in the left valve. These differences give the Triassic forms a distinctive appearance which suggests their generic separation from *Aviculopecten*.

Species referable to the new genus include, besides the type species, the following forms: *Aviculopecten aerarius* Bittner, *benecke*i Bittner, *elegantulus* Bittner, *esinensis* Bittner, *herbichi* Bittner, *interruptus* Bittner, *katzeri* Bittner, and *triadicus* Salomon, and also *Avicula wissmanni* Münster.

ERECTION OF A NEW GENUS *ENSIO* (FAMILY ASTARTIDAE)Genus *ENSIO* gen. nov.

Text-fig. 2

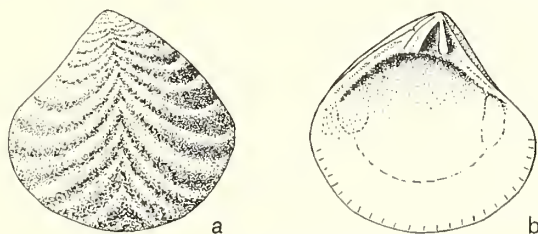
Generic name. Alluding to the ornament of chevrons, suggesting the badge of rank of an N.C.O.; gender, masculine.

Type species. *Ptychomya agassizii* Lycett (1850, p. 408, pl. 11, fig. 6) (synonym, *Astarte divaricata* Etheridge (in Cross 1875, p. 129, pl. 5, fig. 1)), Inferior Oolite.

Diagnosis. Small, suborbicular, some specimens with a trigonal tendency, only slightly inequilateral, compressed; umbo slightly anterior to median, not incurved; escutcheon and lunule narrow and elongate, scarcely impressed, bordered by obtuse ridges. Left valve with two rather elongate, not greatly unequal cardinal teeth diverging to either side of the beak, an acutely triangular recess between them; the anterior tooth separated from the lunular margin by a narrow groove, the posterior tooth fused with the short nymph at its umbonal end; also with a narrow posterior lateral tooth parallel with and close to the adjacent margin. Right valve with a moderately strong median cardinal and

a thin anterior lateral received in the corresponding recesses in the other valve. Ventral margin faintly denticulate internally. Ornament of rounded, chevron-shaped ridges pointing towards the umbo.

Remarks. The holotype of the type species of *Ensio*, *Ptychomya agassizii*, from the Inferior Oolite, Oolite Marl, of Nailsworth, Glos., is in the Geological Survey Museum (reg. no. 9139). A topotype is in the same Museum (no. 99256), while two further specimens from the same formation, recorded as coming from 'Stroud' but possibly also topotypes, are in the E. Witchell Collection in the British Museum (Natural



TEXT-FIG. 2. *Ensio agassizii* (Lycett), Bajocian, Santon, Lincs. Holotype of *Astarte divaricata* Etheridge (Geol. Surv. Mus., Geol. Soc. Coll. no. 7044), a left valve; exterior and interior, $\times 4$.

History). The holotype of *Astarte divaricata*, which is undoubtedly conspecific with *Ptychomya agassizii*, came from the Lincolnshire Limestone of Santon, Lincs., and is in the Geological Survey Museum (ex Geological Society of London Collection, no. 7044). The species is rare and has not been found outside England.

It is interesting to note that the only other described species of *Ensio* occurs as far afield as Borneo. It is *Astarte eastonii* Vogel (1899, p. 55, pl. 3, figs. 1-8) and was found in beds considered to be Upper Jurassic in age, although the exact stage to which they belong seems still to be uncertain. This species has exactly the same type of ornament as *Ensio agassizii*, except that in one of the figured specimens the chevrons of later growth stages are interrupted by a downward V-bend in the middle. Its umbo is less prominent than in the English species.

The description in the above diagnosis of the hinge-teeth of the left valve of *Ensio* is based on the holotype of *Astarte divaricata*. No reference has, however, been made to an obscure median groove seen in the posterior cardinal of this specimen, as Vogel's (1899, pl. 3, fig. 7) figure of the teeth of the corresponding valve of *E. eastonii*, which otherwise agree well with those of the English species, does not indicate this feature. The description of the dentition of the right valve of the new genus has been based on Vogel's fig. 8. Vogel mentions and figures fine transverse striations on the sides of the cardinal tooth of the right valve and of the corresponding socket between the two cardinals of the left valve. These are not visible in the left valve of *E. agassizii*, but its interior is a little eroded.

The hinge of *Ensio* is that of a typical member of the Astartidae, and the entire pallial line and internally denticulate margins also support its reference to that family. It is interesting to find surface ornament of chevrons, like that of certain Veneridae and Lucinidae, in an astartid.

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THE PALAEOECOLOGY OF THE FORAMINIFERA OF THE CHALK MARL

by T. P. BURNABY

ABSTRACT. The frequencies of benthonic foraminifera from twenty-seven samples from the Chalk Marl at Barrington, Cambridgeshire, have been used in constructing a discriminant function which gives a relative measure of the depth of water of the Chalk Marl sea.

THE work here described was carried out in 1950–2, at a time when most of the references cited below had not yet been published. Hence the nature of the plan of work, which was to make a detailed investigation of a single short stratigraphical profile, to develop a suitable quantitative technique, and to evaluate the degree of accuracy of the results. This, though limited in scope, was felt to be a worth-while preliminary to possible future regional palaeogeographical studies, such as that since carried out by R. P. S. Jefferies on the *plenus* Marls of the Turonian (this volume).

The Chalk Marl in Messrs. Eastwood's cement quarry at Barrington is, except for intermittent talus slopes, completely exposed from the Cambridge Greensand at the base to the Burwell Rock at the top. The management's permission having been obtained, twenty-seven samples of chalk were collected from twenty-three different levels in the 90-foot thickness of the *Schloenbachia varians* Zone. Each sample was a discrete lump of chalk and not an aggregate of chippings from an extended vertical surface, the object of study being the actual death assemblages of foraminifera. The penalty incurred in this procedure is, of course, that species occurring abundantly in thin bands but not elsewhere will probably be missed.

About 200 c.c. of chalk from each sample was disaggregated in water, using a shaking machine and four rubber bungs in the glass jars to act as mill-balls, and yielded in the washings from a few thousand to tens of thousands of benthonic foraminifera in the size fraction 1 mm.–0.2 mm. Owing to the presence of some 15–30 per cent. of clay in the Chalk Marl, disaggregation is particularly easy, and no boiling or other treatment is necessary to yield clean undamaged tests. The Burwell Rock is more difficult.

Standard sample counts of from 1,000 to 1,500 specimens were carried out on the benthonic foraminifera in the size fraction 1 mm.–0.2 mm. A specially designed two-stage rotary sample splitter was used to divide the dry sieved washings from a given sample into random subsamples, the accuracy of counting being checked by the χ^2 test. The results of about twenty such tests showed conclusively that the sample counts are as accurately repeatable as random sampling will allow, provided that the specified size limits of the material are not changed. It has also to be remembered that only a single observer was being tested. Some χ^2 tests were also made with data from duplicated extraction processes from a single Chalk Marl sample, the repeatability of the extraction process being thus checked. No significant discrepancies were found. Strongly significant χ^2 values were obtained from five replicated samples collected a few feet apart horizontally at the same level (samples 2/7A–E).

The main results are summarized in the accompanying distribution chart (text-fig. 1). Altogether 49 species were distinguished, of which 44 were regularly recorded in the sample counts. The actual total number present, as estimated by fitting a negative binomial to the observed distribution, could well be about 60: this allows for those species which may have escaped unobserved in thin bands not sampled or, if very rare, in the actual samples. It will be seen that the general aspect of the fauna is fairly constant throughout the section, nearly all the more abundant species, and some of the rarer ones as well, being present at all levels sampled. Arenaceous species represent about half the fauna in terms of individuals and about one-third in terms of species. The zonal index-fossil, *Textulariella cretosa*, is absent from three samples in the first 10 feet of the section. The distinctive Cenomanian species *Cibicides formosa* occurs sparsely in samples 1/13 and 2/7A-E and nowhere else, its maximum level of abundance being 12 per mil.

In warm subtropical seas at the present day, a large proportion of arenaceous individuals and species is characteristic of the faunas occurring in depths of from 5 to 50 fathoms (see, for example, Bandy 1956, charts 5-7). In addition to the arenaceous forms there is often a striking diversity of genera and species of other families in this range of depths (Lowman 1949, p. 1956). The Lagenidae would not be so abundant in this depth range at the present day as they are in the Chalk Marl fauna, but it is well known that in the Mesozoic the Lagenidae were much more widely distributed than they are now, and the principal Chalk Marl genus, *Lenticulina*, is frequently found today at 50 fathoms and less. The principal apparent anomaly concerns the planktonic species, which were not included in the sample counts but which are very abundant in the Chalk Marl. Formerly this might have been taken as indicating a depth of two or three hundred fathoms or more; but recent work has shown that a large proportion of planktonic individuals is by no means unusual in comparatively shallow water. Thus Bandy (1956) records 70 per cent. planktonic forms at a little over 40 fathoms off St. Petersburg, Florida, and Bandy and Arnal (1957) record 25 per cent. planktonic forms at 10 fathoms at two stations off the west coast of Central America.

It will be understood that the palaeoecology of Cretaceous foraminifera is a very different proposition from the comparatively straightforward approach which is possible in the case of the Tertiary. The faunas have been much changed through extinctions and fresh evolutionary speciation, and we are forced to rely upon comparisons of related genera, rather than of species. A further difficulty has been that, until recently, ecological studies of living foraminifera have tended to concentrate upon temperate and cold-water faunas, which have no affinities with the Chalk Marl fauna; indeed at the time the present work was begun it was found that the only reports having any real relevance were the classic papers of Norton (1930) and Lowman (1949).

Fortunately, geological evidence of conditions of deposition of the Chalk Marl is not lacking: the Cambridge Greensand at the base clearly represents a shallow-water phase when the bottom sediments were winnowed by currents, and at the top of the section the Burwell Rock equally clearly represents a time of shallow-water conditions. It is a fair inference that the period of time intervening, during which 90 feet of Chalk Marl was deposited, represents an environment in which the water was somewhat deeper. We have therefore to seek for Chalk Marl foraminifera whose vertical distribution-patterns possess marked peaks or troughs, which might suggest that their relative abundance was governed by the changing environment. The four species *Arenobulimina*

(*Hagenowella*) *anglica*, *Textularia subconica*, *Tritaxia pyramidata* s.l., and *Gyroidinoides nitida*, are particularly noteworthy in this respect, as may be seen from text-fig. 1. Now it is interesting that the living species *Valvulina oviedoiana*, which is perhaps the closest living relative of the Chalk Marl *Arenobulimina* spp., is at the present day largely confined to very shallow warm water, from 0 to 5 fathoms in the West Indies (Norton 1930).

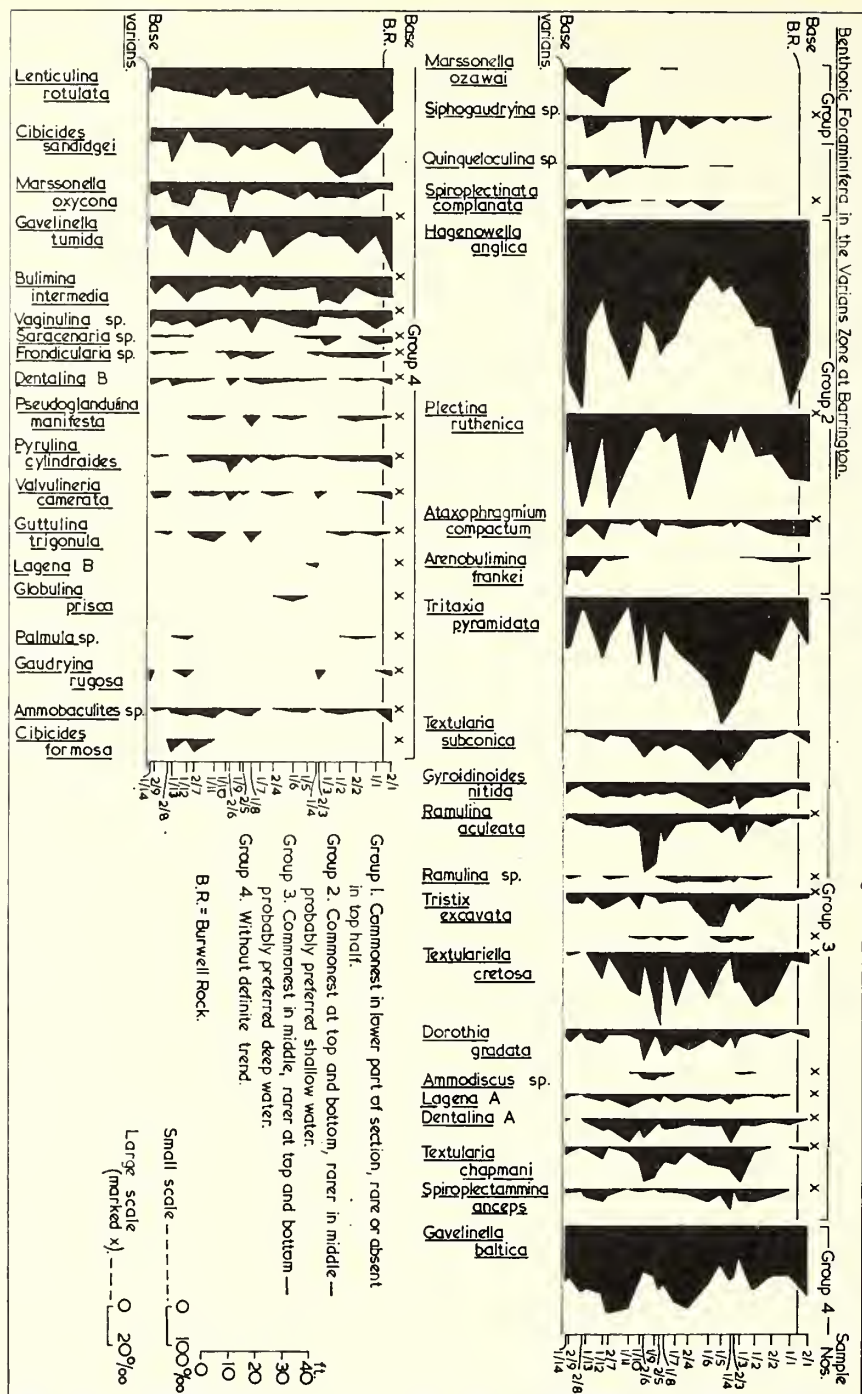
Textularia today is characteristically a genus whose species prefer a depth of the order of 20 fathoms, though naturally among the many living forms there are numerous exceptions. As a rough generalization it would be correct to say that they are relatively uncommon in very shallow water or at depths much below 100 fathoms. (See, for example, Norton 1930; Lowman 1949, figs. 13, 15, and 17; Walton 1955, figs. 20–21; Bandy 1956, charts 1–7; Bandy and Arnal 1957, table 1.)

Living species of *Gaudryina* in which a large part of the test is triserial and triangular in cross-section, resembling in this respect the extinct genus *Tritaxia*, occur mostly in moderately deep water, from 50 to 500 fathoms. Of fourteen Recent species listed by Cushman (1937) none are recorded from depths of less than 17 fathoms. Two Californian species listed by Walton (1955) occur at depths of between 12 and 120 fathoms. Bandy and Arnal (1957) report *G. atlantica* at depths ranging from 30 to 57 fathoms. It is arguable that the Cretaceous *Tritaxia* is not more closely related to these Recent species than is implied by its inclusion in the same family, but in any case the present-day bathymetric distribution of the Verneuilinidae is much the same as that of *Gaudryina*. We conclude, therefore, that *Tritaxia pyramidata* s.l. most probably preferred a moderately deep-water habitat.

Gyroidina (including *Gyroidinoides*) is a deep-water form at the present day. The shallowest occurrences I have found recorded are at 60 fathoms in the Gulf of Mexico (Norton 1930, Lowman 1949). It is common at abyssal depths (Bandy 1953, p. 171 and table 1).

Now, if it is conceded that the relative abundance of the four Chalk Marl species, *Hagenowella anglica*, *Textularia subconica*, *Tritaxia pyramidata*, and *Gyroidinoides nitida*, was governed largely by the depth of water, then the immediate conclusion will be drawn that there was a deep-water phase in the deposition of the Barrington Chalk Marl, culminating at a horizon about 60 feet above the base of the section, where the depth of water was perhaps 50–100 fathoms. At the commencement and end of Chalk Marl time, the sea appears to have been only about 5 fathoms deep. It seems to have remained fairly shallow while the first 40 feet of the Chalk Marl was laid down, although conditions then appear to have been extremely unsettled. The same four species show clearly enough by their change in relative abundance the shallowing of the sea during the last phase of Chalk Marl deposition, represented by the topmost 25 feet of the section below the Burwell Rock.

It is possible to make use of the observed frequencies in the samples of the foraminifera in constructing a cinematic record of the changes in depth of the Chalk Marl sea, not by purely subjective assessment but by statistical analysis of the data. The basic idea is to obtain a suitably weighted average of the percentages of the four species at any given horizon, the value of which serves as a measure of the former depth of the sea at that horizon. The weighted average, known as a discriminant function, is of course expressed in arbitrary units which must be assumed to be simply proportional to the depth in fathoms.



Essentially the same method has already been employed by N. M. Curtis, Jr. (1955) in plotting an oscillation chart of the changes in depth of the Eocene sea in a section in the Weches formation in Texas. His discussion of the palaeoecology is naturally not confined to the two abundant depth-sensitive species, *Quinqueloculina claiborniana* and *Siphonina claibornensis*; however, it seems clear from his remarks below his fig. 2 that the oscillation chart shown thereon has been constructed by taking, at each sampling point, a simple average of the percentage frequencies of the two species, with weighting coefficients (−1, 1), as a measure of the depth.

The procedure adopted for the four Chalk Marl species was as follows. From the frequencies per mil. (x_{jk} specimens) of the j th species in the k th sample, were subtracted the values of a five-point moving average representing the trend-line of the species concerned, giving the residuals (i.e. deviations from trend)

$$z_k = x_k - \frac{1}{5}(1, 2, 3, \dots)(x_{k-2} \dots x_{k+2}).$$

The 4×4 matrix of residual variances and covariances for the four species was then calculated, having elements w_{ij} such that

$$w_{ij} = \frac{1}{N-4}(z_{ik} z_{jk}),$$

the alternate sub- and superscript $_{ik}^{jk}$ denoting summation over the range of k , which in this case is from $k = 3$ to $k = N-2$, since the moving average does not cover the first and last two samples. There are 23 horizons sampled, but only $19 = N-4$ terms in the mean products, w_{ij} , the 16 values of which are as follows:

	<i>Gyroidinoides</i>	<i>Textularia</i>	<i>Tritaxia</i>	<i>Hagenowella</i>
<i>Gyroidinoides</i>	73.6	51.2	63.7	−155.5
<i>Textularia</i>	51.2	159.2	−18.2	−282.4
<i>Tritaxia</i>	63.7	−18.2	2324.7	−851.1
<i>Hagenowella</i>	−155.5	−282.4	−851.1	2234.7

This residual dispersion matrix can be regarded as giving the variances and covariances within a generalized thin stratum of Chalk Marl roughly 10 feet thick.

The next step is to select—subjectively—on general geological grounds which will now be apparent, two small groups of samples representing deep-water and shallow-water conditions respectively. Group DW comprised Nos. 1/6, 1/5, 1/4, 2/3, and 1/3, and Group SW Nos. 1/14, 2/9, 2/8, 1/13, and 1/1. As a defence against possible criticism, it may be remarked that the precise choice of particular samples makes little difference to the results, since the residual dispersion matrix is not thereby affected. The mean frequencies per mil. from the two groups of samples were calculated, and from them the set of differences $d_i = \bar{x}_{iDW} - \bar{x}_{iSW}$ was obtained.

$$(d_i) = \begin{bmatrix} 36.2 \\ 83.0 \\ 204.0 \\ -236.0 \end{bmatrix} \begin{matrix} \textit{Gyroidinoides} \\ \textit{Textularia} \\ \textit{Tritaxia} \\ \textit{Hagenowella}. \end{matrix}$$

The discriminant function was then calculated in the usual way (see, for example, Rao 1952, p. 254) by solving the set of four simultaneous equations

$$\lambda_j w^{ij} = d_i$$

the solutions obtained being

$$\lambda_j = (0.0535, 0.508, 0.0888, -0.00393)$$

and the discriminant function is thus

$$X = 0.0535x_1 + 0.508x_2 + 0.0888x_3 - 0.00393x_4$$

where the variates $x_1 \dots x_4$ are the frequencies per mil., in any one sample of Chalk Marl, of the four species of *Gyroidinoides*, *Textularia*, *Tritaxia*, and *Hagenowella*. Values of X so calculated have the smallest possible residual variance relative to their variance between samples from deep and shallow water.

The mean values $\bar{X}$ for the deep-water and shallow-water groups of samples, when differenced, give the value of the statistic known as D^2 . We have

$$\bar{X}_{DW} - \bar{X}_{SW} = 70.77 - 8.01 = 62.76 = D^2.$$

The square root of D^2 gives the standard error of the value of X for a single sample, which is therefore $\sqrt{(62.76)} = 7.922$.

It is interesting to note that the standard deviation of X can be estimated directly from the five replicated samples, Nos. 2/7A-E. From the five values of X (see Table 1) we obtain in the usual way $s_X = 6.15$, with 4 degrees of freedom, which shows that the previous result is of the right order of magnitude.

Returning to the Chalk Marl sea, it is clear that we do not know, nor can we discover directly, what value of X corresponds to a particular depth in fathoms. But if we care to postulate that the value of X is linearly related to the depth of water, and assign the notional depths of 50 and 5 fathoms to the deep-water and shallow-water groups, we can set up the equation

$$Y_k - 5 = (50 - 5)(X_k - \bar{X}_{SW}) / (\bar{X}_{DW} - \bar{X}_{SW})$$

where Y_k is the depth in fathoms corresponding to the value of X_k for the k th sample. Most of the Chalk Marl samples will now be found to lie somewhere in the range 5 to 50 fathoms which we had previously concluded to be about right. Since we now have the value of the constant of proportionality between X and Y , we can determine the standard error of Y : it is

$$s_Y = s_X(45)/(62.76) = 45/\sqrt{(62.76)} = 5.680 \text{ fathoms.}$$

(Note. A standard deviation can only be put to practical use by performing at least one further arithmetical operation upon it: four figures are therefore quoted, out of courtesy to readers—not because it is thought to represent anything but an order of magnitude.)

The values obtained for the depth Y for the twenty-three sampled horizons in the Barrington Chalk Marl are given in Table 1. Also shown are the heights in feet of the sampling points above the base of the formation, the total number of benthonic foraminifera extracted per c.c. of chalk, and (measured for 16 samples only) the percentage of insoluble mineral residues present in the chalk.

There is a rather sharp drop in the insoluble fraction at around 50 feet above base,

TABLE 1

<i>Sample</i>	<i>Height (ft.) above base</i>	<i>X</i>	<i>Y (fathoms)</i>	<i>Forams/c.c. chalk</i>	<i>% insol. residue</i>
Group SW	..	8.01	5.0		
Group DW	..	70.77	50.0		
2/1	90.0	25.91	17.8	17.1	8.2
1/1	84.5	3.00	1.4	26.3	20.3
2/2	77.5	22.83	15.6	26.7	..
1/2	70.5	22.14	15.1	35.5	13.8
1/3	65.5	63.64	44.9	34.0	18.1
2/3	63.5	66.35	46.8	43.3	..
1/4	62.5	81.21	57.5	..	13.1
1/5	59.5	68.43	48.3	46.3	16.8
1/6	56.0	74.53	52.7	47.0	17.3
2/4	46.5	41.44	29.0	30.8	..
1/7	42.0	31.49	21.8	41.1	23.9
1/8	39.0	32.61	22.6	21.6	21.2
2/5	35.5	30.42	21.1	33.9	..
1/9	34.5	40.38	28.2	21.2	26.6
2/6	30.0	41.82	29.2	25.9	..
1/10	29.0	41.89	29.3	21.5	23.5
1/11	26.0	12.51	8.2	34.6	25.9
2/7	17.0	13.74	9.1	80.0	..
1/12	15.0	29.30	20.3	73.7	19.7
1/13	9.0	7.68	4.8	149.0	30.4
2/8	7.5	1.58	0.4	168.0	..
2/9	2.5	12.71	8.4	122.0	26.6
1/14	2.0	15.08	10.1	158.0	24.4
2/7A	17.0	12.23	8.0	98.6	
B	..	15.93	10.7	115.0	
C	..	21.17	14.4	..	
D	..	4.79	2.7	26.7	
E	..	17.51	11.8	..	

Explanation of Table 1. The Chalk Marl section at Barrington. Serial numbers of the samples, their heights above the base of the formation, values of the discriminant *X*, the assumed equivalent depths of water *Y*, the numbers of benthonic foraminifera (larger than 0.2 mm. diameter) per c.c. of undisaggregated chalk, and the percentages by weight of mineral residue insoluble in HCl. At the head of the table are given the mean values of *X* and the assumed values of *Y* for Group SW (the four samples from 2 to 9 feet above base plus sample 1/1), and Group DW (the five samples from 56–66 feet above base). The five replicated samples 2/7A–E were collected a few feet apart horizontally at the same level, $\pm$ a few inches either way.

and it is tempting to associate this with the rapid increase in Y to over 50 fathoms, as though the coastline were receding in consequence of a general rise in sea-level. The next sharp drop in the insoluble fraction occurs at 90 feet, in the topmost sample which is from the Burwell Rock. The value of Y of 17·8 fathoms for this sample is, however, almost certainly not to be relied on, since from the abundance of shell-debris in the washings, and the battered appearance of the foraminifera, it is obvious that there has been sedimentary reworking of the material. The topmost sample but one, at 84·5 feet, which is still within the Chalk Marl, gives a value of Y of only 1·4 fathoms, and I would conjecture that the true depositional environment of the Burwell Rock was even shallower than this.

In the lowest part of the section, from 0 to 20 feet above the base, the number of foraminifera in unit volume of chalk is exceptionally high. The simplest explanation is that this reflects an exceptionally low net sedimentation rate, the numbers of foraminifera living and reproducing per unit area of sea-floor supposedly remaining roughly constant. The values of Y recorded in this part of the section indicate irregular and pronounced fluctuations in depth, the average being about 10 fathoms but with occasional very shallow episodes. Under these conditions it would not be surprising if the sedimentary record were somewhat condensed. That the Barrington section is condensed is suggested also by the much greater thickness of the Chalk Marl elsewhere; e.g. 120 feet in Oxfordshire, while bore-hole records near Cambridge also seem to indicate thicknesses greater than 90 feet.

It now becomes interesting to examine the behaviour of some of the other species of foraminifera, in the light of the above results. *Lenticulina rotulata* is an abundant species which apparently was affected very little by the disturbed conditions in the first 20 feet of the section. It thus appears reasonably certain that the hypothesis of a low net sedimentation rate is correct, since otherwise we would have to suppose that the percentage of *Lenticulina* kept exactly in step with pronounced changes in the total number of foraminifera per unit area of sea-floor.

Quinqueloculina sp. and *Marssonella ozawai* are both confined to the lower part of the Chalk Marl. *Quinqueloculina* is common only in samples 1/13 and 2/7A, B, C, and E: it is rare in samples 2/8 and 2/7D. Present-day species of the genus are generally common in shallow-water inshore environments, and there are some that tolerate slightly brackish water. *Marssonella ozawai* has a more restricted stratigraphical range, which makes me reluctant to draw any inferences; but it may be worth noting that it is most abundant in sample 1/12, for which $Y = 20\cdot3$ fathoms and the per cent. insol. residue is 19·7, figures which stand out from the general trends of about 7 fathoms and 28 per cent. respectively at about that horizon (see Table 1).

Arenobulimina frankei occurs only in the lower 20 feet and the upper 20 feet of the section. It is absent from sample 1/12. It seems definitely to be a shallow-water species.

Plectina ruthenica is present throughout the section being most abundant in samples with a low value of Y .

Dorothia gradata, *Textulariella cretosa*, *Textularia chapmani*, *Ramulina* (two species) and *Tristix* (two species) and perhaps also *Spiroplectammina anceps*, show a preference for samples with a high value of Y .

Gavelinella baltica seems to have had no ecological preferences either way.

Lenticulina rotulata and *Cibicides sandidgei* are most abundant towards the top of

TABLE 2

	2 3	1 3	1 2a	1 2b	2 2	1 1	2 1	Total no. specimens observed
	63½	65½	70½	—	77½	84½	90	
<i>Ammodiscus</i>		1						12
<i>Ammobaculi</i>		1	2	3	1		7	57
<i>Spiroplectan</i>		6	9	8	5			118
<i>Textularia s</i>	88	74	21	32	18	1	31	1,395
<i>Textularia c</i>	15	18	2	3			2	192
<i>Tritaxia pyr</i>	808	260	146	191	202	50	128	5,457
<i>Spiroplectin</i>			1					36
<i>Gandryina r</i>	3						2	22
<i>Siphogaudry</i>	2			5				112
<i>Arenobulini</i>	207	203	331	409	346	567	370	10,729
<i>Arenobulini</i>				2	6	8	1	311
<i>Ataxophragi</i>	3		7	1	9	9	9	117
<i>Plectina ruth</i>	17	4	24	31	24	40	37	821
<i>Dorothia gra</i>	53	20	8	10	20	1	14	889
<i>Marssonella</i>	34	33	40	51	46	11	14	1,065
<i>Marssonella</i>								635
<i>Textulariella</i>	18	15	35	37	27	5	7	461
<i>Quinquelocu</i>				1				308
<i>Lenticulina r</i>	61	61	104	115	103	176	117	2,601
<i>Marginulina</i>	3	7	9	15	16	8	8	170
<i>Saracenaria</i>		4		1		4	2	22
<i>Vaginulina s</i>	3	3	3	4	2	10	3	222
<i>Palmula sp.</i>					1			3
<i>Fronicularia</i>		1	4		2	2		29
<i>Dentalina A</i>	9	3	1	6	1			164
<i>Dentalina B</i>	1			1	1	2	3	39
<i>Pseudogland</i>			1		2	1		16
<i>Tristix excav</i>	6	10	1	2	2	4	2	179
<i>Tristix B</i>		1						15
<i>Quadratina s</i>								1
<i>Lagea A</i>	2	2			1			76
<i>Lagea B</i>								1
<i>Ramulina ac</i>	8	14	5		7	1	2	249
<i>Rauulina B</i>	2		1	1				29
<i>Pyrulina cyl</i>		1	2	3	2	2	6	58
<i>Guttulina tri</i>			1	1		1		34
<i>Globulina pr</i>								4
<i>Bulimina int</i>	14	11	15	20	6	12	10	286
<i>Valvulineria</i>	3					1	3	35
<i>Gyroidinoide</i>	29	63	38	43	36	13	23	1,151
<i>Gavelinella b</i>	50	78	207	249	171	152	193	6,114
<i>Gavelinella c</i>	11	10	8	17	23	11	30	385
<i>Cibicides for</i>								39
<i>Cibicides cf.</i>	44	95	147	186	138	71	14	1,912
Totals,	994	—1	173	448	218	163	038	36,571

Explanation: * from the same field sample: samples 2/7A-E are replicate were counted as 1 if more than half complete; otherwise as

TABLE 2

SPECIES	Section Sample Height above base, ft.	1	2	2	1	1	2	2	2	2	2	1	1	2	1	2	2	1	1	2	1	1	1	2	1	1	1	2	1	1	2	Total no. specimens observed	
		14	9	8	13	12	7A	7B	7C	7D	7E	11	10	6	9	5a	5b	8	7	4	6	5	4a	4b	3	3	2a	2b	2	1	1		
		2	2½	7½	9	15	17	—	—	—	—	26	29	30	34½	35½	—	39	42	46½	56	59½	62½	—	63½	65½	70½	—	77½	84½	90		
<i>Ammodiscus</i> sp.														1	3	3	2		2							1						12	
<i>Amnobiaulites</i> sp.			1		3	4	5			5	1	5		1	3	6	4	3			1	1				1						7	57
<i>Spiroplectanumina anceps</i> (Reuss 1845)		2	1	1	6	10	2	1	2	4	3		1	2			2	2	2	2	8	2	27	10		6	9	8	5			118	
<i>Textularia subcuvica</i> (Franke 1928)		8	5	2	14	41	8	4	10	1	11	28	61	84	46	65	43	57	44	61	115	86	195	141	88	74	21	32	18	1	31	1,395	
<i>Textularia chapmani</i> Lallieker 1935		6	2		2	10		1		1		5	10	20	20	19	12	8	11	3	10	12			15	18	2	3			2	192	
<i>Tritaxia pyramidata</i> s.l. (Reuss 1863)		218	146	31	54	240	90	165	111	56	106	14	203	45	261	248	113	91	172	201	247	397	578	385	308	260	146	191	202	50	128	5,457	
<i>Spiroplectinata complanata</i> (Reuss 1860)		5	5		6			1	2	2	2			1			1		4		5					1						36	
<i>Gaudryina rugosa</i> d'Orbigny 1840		10				5	1										1								3						2	22	
<i>Siphogaudryina</i> sp.		1	2		17	10	6	1	1	1	7	3		25	2	1	6	11	1	7		3			2							112	
<i>Arenobulimina (Hagenowella) anglica</i> Cushman 1936		553	495	589	446	306	285	354	162	344	219	544	386	290	353	637	404	379	362	257	160	222	323	226	207	203	331	409	346	567	370	10,729	
<i>Arenobulimina</i> cf. <i>frankel</i> Cushman 1936		119	31	36	79			1	9	2	17															2	6	8	1			311	
<i>Ataxophragminum compactum</i> Brotzen 1936		12	10	3	2	15		3				3		5	10		1	2	2	5	2	4			3		7	1	9	9		117	
<i>Plectina ruthenica</i> (Reuss 1850)		29	13	58	67	13	59	46	34	45	57	29	15	10	7	18	10	15	11	56	13	24	10	5	17	4	24	31	24	40	37	821	
<i>Dorothia gradata</i> (Berthelin 1880)		34	37	6	35	42	7	31	10	4	9	20	32	92	17	40	32	76	48	62	25	52	26	26	53	20	8	10	20	1	14	889	
<i>Marssonella oxycona</i> (Reuss 1860)		27	31	23	74	94	5	13	22	9	22	29	33	95	15	39	24	33	21	27	52	26	86	36	34	33	40	51	46	11	14	1,065	
<i>Marssonella ozawai</i> Cushman 1936		38	46	76	97	155	21	96	21	45	37						3															635	
<i>Textulariella cretosa</i> Cushman 1932			1		21	3				1		24	26	6	34	70	42	4	34	7	27	9	3	5	18	15	35	37	27	5	7	461	
<i>Quinqueloculina</i> sp.		12	8	9	64	1	36	22	51	8	52	5	7	1	5	11	3	5	5			2										308	
<i>Lenticulina rotulata</i> Lamarck 1804		92	53	61	81	101	73	53	43	104	48	100	58	79	84	101	70	96	97	67	54	156	96	61	61	104	115	103	176	117		2,601	
<i>Marginalina</i> sp.		2	1				2			4		8	11	10	5	15	12	9	6	14	5				3	7	9	15	16	8	8	170	
<i>Saracenaria</i> sp.		2	1	1		1			1												1	2	2		4	7	1				4	2	
<i>Vaginulina</i> sp.		15	7	8	12	8	7	6	4	19	8	7	4	8	4	7	7	12	3	5	9	10	14	10	3	3	3	4	2	10	3	222	
<i>Palmla</i> sp.						2																										3	
<i>Froncularia</i> sp.			1		1					1			1	3	1		2	4	2				2	2			1	4		2	2	29	
<i>Dentalina</i> A		3			3	8	6	3	4		9	15	7	11	5	4	2	7	5	4	5	4	29	10	9	3	1	6	1			164	
<i>Dentalina</i> B		4	2		4	2	1			3							1	4	2	1	1			2	1		1	1		2	3	39	
<i>Pseudoglandulina manifesta</i> (Reuss 1851)						2			1	1	1	1				1		4			1								2	1		16	
<i>Tristix excavata</i> (Reuss 1863)		3	6	6	1	12	6	5	6	6	9	1	9		2	11	2	5	4	5	18	20	9	6	6	10	1	2	2	4	2	179	
<i>Tristix</i> B													1	1		1	1					2	5	2		1						15	
<i>Quadratina</i> sp.																																1	
<i>Lagena</i> A		4	1		1	4	2			2	4	11	4	4	1	10			3	1	3	1	9	6	2	2						76	
<i>Lagena</i> B																																1	
<i>Ramulina aculeata</i> (d'Orbigny 1840)		4	1	4	7	9	13	10	4	3	4	8	10	34	29	11	5	15	6	4	3	10	8	10	8	14	5		7	1	2	249	
<i>Ramulina</i> B			1				8			2						2	1	3	2	2	2	2						1	1			29	
<i>Pyrulina cylindroides</i> (Roemer 1838)						2			9	1	4	2	3	9	2		1	3	2			1	1	1		1	2	3	2	2	6	58	
<i>Guttulina trigonula</i> (Reuss 1845)				1			5	4			6					14	1											1	1		1	34	
<i>Globulina prisca</i> Reuss 1863						2																2										4	
<i>Bulimina intermedia</i> Reuss 1845		11	10	3	8	19	14	8	13	2	8	7	7	8	4	10	6	12	6	10	8	7		17	14	11	15	20	6	12	10	286	
<i>Valvulineria allomorphinoides</i> (Reuss 1860)			3	2			6		1	2		3		6			4			1				3								35	
<i>Gyrogonioides nitida</i> (Reuss 1845)		41	22	5	18	61	54	18	22	17	34	48	29	36	28	42	36	28	25	49	68	61	96	68	29	63	38	43	36	13	23	1,151	
<i>Gavelinella baltica</i> Brotzen 1942		226	147	211	256	273	341	141	165	292	201	278	171	133	149	282	202	173	241	262	178	119	274	199	150	78	207	249	171	152	193	6,114	
<i>Gavelinella</i> cf. <i>tunida</i> Brotzen 1942		6	9	5	17	31	17	2	1	1	1	21	22	22	14	20	19	8	10	26	14	9			11	10	8	17	23	11	30	385	
<i>Cibicides formosa</i> Brotzen 1945					10		3	7		5	3	11																				39	
<i>Cibicides</i> cf. <i>sandidgeri</i> Brotzen 1936		53	41	50	138	1	56	12	23	59	23	49	58	84	56	70	56	60	60	37	74	41	72	44	44	95	147	186	138	71	14	1,912	
Totals, 1,000+		540	141	191	523	499	128	024	-259	050	-92	274	170	132	160	755	126	129	193	209	123	183	930	309	094	-1	173	448	218	163	038	36,571	

Explanation of Table 2. Observed frequencies (actual numbers of specimens counted) in the size fraction 1 mm.-0.2 mm. Samples nos. 2/5a, b, 1/4a, b, 1/2a, b, are duplicated 'throughputs' from the same field sample; samples 2/7A-E are replicated field samples. Also present in small numbers: *Bulloporea sollasi* (Chapman 1892), *Lenticulina* B, *Fronicularia* B, *Nodosaria* sp., and *Nodosarella* sp. Fragmentary specimens were counted as 1 if more than half complete; otherwise as 0.

the section. This may perhaps indicate a preference for fairly shallow, clear water, not too close inshore. Except in the lower 20 feet of the section, the tests of *Cibicides sandidgei* have a slightly convex spiral side (the umbilical side being, of course, strongly convex), whereas in the lower 20 feet of the section the spiral side is flat. In living forms such as *Cibicides lobatulus* the flat spiral side is known to function as an area of attachment, on which the animal creeps about over algal fronds, hydroids, bryozoa, and so on, which may grow on the bottom in shallow water in the photic zone.

An independent check on the depth of the Chalk Marl sea at Barrington, or failing that, on its temperature, is clearly highly desirable. There is none yet available for the Chalk Marl itself, but Lowenstam and Epstein (1954) give the results of a series of O^{16}/O^{18} analyses of Cretaceous fossils from a number of horizons and localities which include a belemnite and an oyster from the *subglobosus* Chalk of Hampshire ($T = 16.9$ and 25.1° C. respectively), a Cenomanian belemnite from Bornholm ($T = 15.4^{\circ}$ C.), Albian belemnites from Jutland and their associated chalk ($T = 17.3$ and 27.6° C. respectively), and a belemnite and an oyster from the Cenomanian of Hautrage, Belgium ($T = 16.1$ and 27.6° C.).

It is highly satisfactory to find the same range of temperatures in the Gulf of Mexico at the present day at approximately the range of depths which we have inferred for the Chalk Marl, although, of course, the data relate to different horizons and localities and the absence of a discrepancy does not of itself constitute agreement. From data given by Bandy (1956) it appears that in the Gulf of Mexico a temperature range of $24\text{--}30^{\circ}$ C. is characteristic of the bottom water at 5 fathoms, and a temperature range of $16\text{--}22^{\circ}$ C. is characteristic of 50 fathoms.

Emiliani and Epstein (1953) have demonstrated the feasibility of determining O^{16}/O^{18} temperatures for fossil tests of Pleistocene foraminifera, but it would not necessarily be practicable to get results from Chalk foraminifera which differed significantly from the Chalk matrix. Contamination through recrystallization is thought to have introduced an error in at least some of the Cretaceous fossils studied (see Lowenstam and Epstein 1954, pp. 211 and 234). The high temperatures of the order of 30° C. determined for many specimens of the Chalk matrix appeared puzzling at the time; however, it is now known that the Chalk matrix consists of the skeletal disks of planktonic coccospheres (Black and Barnes 1959). The extremely detailed state of preservation of the coccoliths makes it seem unlikely that much, or indeed any, recrystallization has taken place in typical soft chalks of Cretaceous age, although enough carbonate from the coccoliths has doubtless gone into solution to provide an effective contaminant for other fossils. The presence in the Chalk—and in the Chalk Marl of Barrington (my own observations)—of rhabdoliths, which, unlike the coccoliths, are exclusively tropical in distribution at the present day, would make it surprising if the O^{16}/O^{18} analyses did not record fairly high temperatures.

It would be very interesting to make a study of the foraminifera from the sections in the Norwich Chalk for which detailed palaeotemperature records are given by Lowenstam and Epstein. It is possible that the Chalk Marl section described here would repay investigation by the oxygen isotope method, since the inferred range of depth should be sufficient to induce measurable changes in the temperature of the bottom water, though naturally a perfect correlation is not to be expected.

The author's collection is deposited in the Sedgwick Museum, Cambridge.

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THE PALAEOECOLOGY OF THE *ACTINOCAMAX* *PLENUS* SUBZONE (LOWEST TURONIAN) IN THE ANGLO-PARIS BASIN

by R. P. S. JEFFERIES

ABSTRACT. The *plenus* Subzone often conforms to a standard succession of eight beds, numbered 1 to 8 in ascending order. The distribution of aragonitic fossils in the *plenus* Subzone was probably controlled more by preservation than ecology. Preservation was determined firstly by temperature and secondly by turbulence.

In late *subglobosus* times the distribution of macro- and microfauna was governed by depth of water, and the depth preferences of the various species of benthonic foraminifera were like those of their relatives in *varians* times. There was little faunal change at the beginning of Bed 1 times, despite extensive erosion. This indicates that the pre-Bed 1 shallowing, for which there is much lithological evidence, was accompanied by only a small rise in temperature. A sudden change at the beginning of Bed 2 times to a shallower-water type of fauna was due to a considerable rise in temperature which led also to the preservation of aragonitic fossils. The peculiarities of the fauna of Beds 4–6, including the presence of *Actinocamax plenus* and *Oxytoma seminudum*, suggest a moderate decrease in temperature with the appearance of species of Central European Russian affinities. This moderate fall in temperature is reflected in the microfauna. During the deposition of Beds 7 and 8 the temperature rose again slightly.

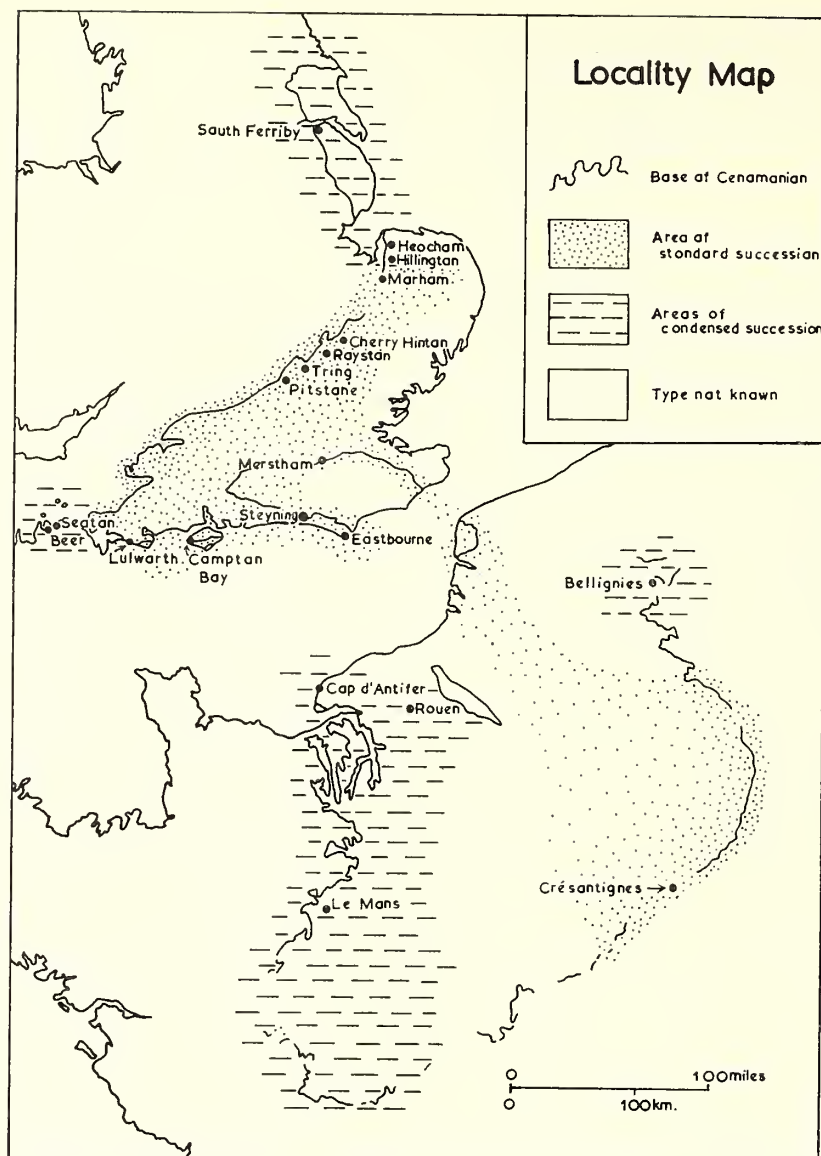
On the basis of certain simplifying assumptions the temperature of deposition of Bed 1 was probably below 5–10° C., that of Beds 4–6 about 16–9° C. and that of Bed 2 considerably higher than 16–9° C.

IN most of the Anglo-Paris Basin the *Actinocamax plenus* Subzone of the *Inoceramus labiatus* Zone is a band of conspicuous marls and marly chalks at the top of the Lower Chalk immediately beneath the Melbourn Rock. It should probably be placed at the base of the Turonian. The stratigraphy of the Subzone has been discussed in detail elsewhere (Jefferies 1961) so that only a short stratigraphical summary is necessary.

In the middle of the Anglo-Paris Basin the *plenus* Subzone conforms more or less to a standard succession of eight beds, numbered 1 to 8 in ascending order and recognizable by fauna and lithology. The type of this standard succession is taken at Merstham in Surrey, on the scarp of the North Downs, and the succession at Merstham is summarized in text-fig. 2. Important features of the succession are (i) the erosion surfaces beneath Beds 1, 2, 4, 6, and 8, especially those beneath Beds 1 and 4; (ii) the marked faunal change at the base of Bed 2; (iii) the occurrence of certain species, including *Actinocamax plenus*, in Beds 4–6; and (iv) the occurrence of the two ammonite faunas—that of *Metoicoceras geslinianum* in Beds 1 to 3 and that of *M. gourdoni* in Beds 4 to 8.

Towards the edges of the Anglo-Paris Basin the *plenus* Subzone is condensed or absent and rests upon, or wedges out against, a sub-*plenus*/*labiatus* erosion surface, homotaxial with the erosion surfaces of the standard succession (text-fig. 1). There is evidence to suggest that the muddiness of the *plenus* Subzone is connected with shallow water and directly associated with the numerous erosion surfaces of the standard succession and with the way in which the Subzone wedges out peripherally (Jefferies 1961).

The purpose of this paper is to discuss the ecology of the *plenus* Subzone fauna, and, in particular, to explain the faunal change at the base of Bed 2, and the faunal peculiarities (including the presence of belemnites) of Beds 4–6. This discussion is based



TEXT-FIG. 1. Locality map. This map shows only those localities from which fossils are mentioned in the present investigation.

partly on detailed bed-by-bed collecting and partly on the application to the foraminifera of those 'pollen-analytical' methods which have been so successful in the study of the Quaternary and which Burnaby (1961) has used in his work on the *varians* Zone.

The Type of the Standard Succession at Merstham.			
Scale in ft.	Important Macrofossils (Ammonites excepted).	Aragon. Fossils.	Ammonites.
M.R. ES			
8 ES	As 7, but without <i>O. wiesti</i> , <i>C. hirudo</i> .	Rare	Gourdoni Zone.
7b ES	As 4-6 but without fossils marked *.		
7a	<i>Orbirhynchia wiesti</i> abundant, <i>Cidaris hirudo</i> common.		
6 ES		Abundant	Kanabicerias sp., Sciponoceras sp.
5	As Bed 2, 2-3 & 3 but with <i>Act. plenus</i> *(c.), <i>Oxytoma seminudum</i> *, <i>Aequipecten arlesiensis</i> *, <i>Ditrupea difformis</i> *, <i>Plicatula barroisi</i> much commoner than below or above.		
4ii			
4i		None	Geslinianum Zone.
3b	As 2 & 2-3 but all fossils rarer, especially calcitic ones.		
3a	<i>Rhynchonella</i> 'lineolata carteri', <i>Entolium membranaceum</i> , <i>Calliderma smithiae</i> , <i>Grammatodon</i> cf. <i>cenomanense</i> , <i>Aporrhais</i> sp., <i>Solarium</i> sp., <i>Dentalium</i> sp. Large, grypheate <i>O. vesicularis</i> common in Bed 2, absent above.		
2-3		None	Metoicoceras geslinianum (c.), Scaphites equalis, Austiniceras dibleyi.
2b			
2a	Marked faunal change.		
1b	As <i>subglobosus</i> Zone, but <i>Ostrea vesicularis</i> larger (3 cm.), <i>Orbirhynch. multicostrata</i> common, <i>Ctenothrissa</i> sp. and <i>Scapanorhynchus subulatus</i> common. 'Trachyster' cf. <i>rugosus</i> present but rare. <i>Holaster trecensis</i> rarer than in <i>subglobosus</i> Zone and <i>Plicatula inflata</i> probably extinct.	None	
1a			
Subgl-obosus Zone.	<i>Ostrea vesicularis</i> (c.) (about 1 cm. long), <i>Holaster trecensis</i> (c.), <i>Lingula</i> sp. (c.), <i>Lima globosa</i> , <i>Problematicum</i> sp., <i>Aequipecten beaveri</i> , <i>Entolium orbiculare</i> , <i>Neitheia quinquecostata</i> , <i>Plicatula inflata</i> .		

TEXT-FIG. 2. The standard succession at Merstham, Surrey (type locality). ES, erosion surface.

PRESERVATION OF ARAGONITIC FOSSILS IN THE *PLENUS* SUBZONE

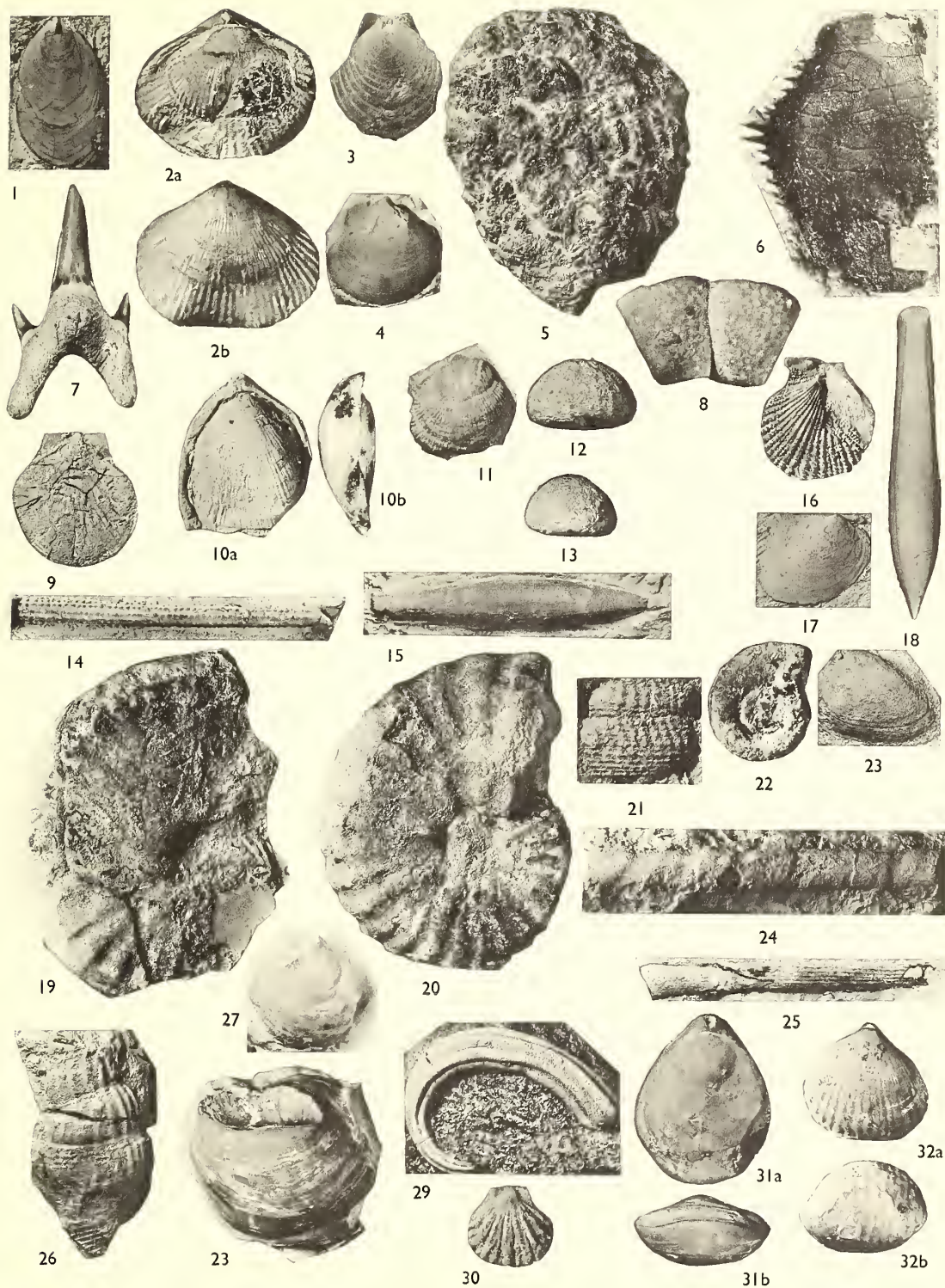
Aragonitic fossils may be preserved in the *plenus* Subzone and Upper *subglobosus* Zone in three main ways which can be called 'normal', 'pebble', and 'oyster-cast' preservation.

'Normal' preservation is the commonest type in the standard succession and also occurs in the *varians* Zone and lower *subglobosus* Zone. Normally preserved aragonitic fossils have the shell converted to marcasite or pyrite (which has since usually turned to limonite) or to chalky calcite and when calcitized are often thinly green-coated. Also they are filled with rock of the same age and type as the matrix, and, except when the matrix is hard, show plastic compression perpendicular to the bedding plane.

'Pebble' preservation is commonest in condensed successions, as in Devon. Pebble fossils are filled with rock which is evidently older and somewhat harder than the matrix and fragments of this older rock may cling to the outside of the fossils. The fossils are usually thickly green-coated or somewhat phosphatized (indicating long exposure on the sea floor), are not plastically compressed, and tend to hammer out rather easily from the matrix.

EXPLANATION OF PLATE 77

- Figs. 1–8. Cold-water group (Bed 1 and the *subglobosus* Zone). 1, *Lingula* sp., $\times 6.7$; Bed 1, Merstham. 2, *Orbirlhynchia multicosata* Pettitt, $\times 1.33$; *a* brachial, *b* pedicle valve aspect; Bed 1, Merstham. 3, *Entolium orbiculare* (Sowerby), $\times 2$; Top *subglobosus* Zone, Cernay-en-Dormois (Ardennes). 4, *Lima globosa* (Sowerby), $\times 2$; Top *subglobosus* Zone, Merstham. 5, Problematicum, $\times 1$; Bed 1, Merstham. These structures consist of coarse sand grain-size microfossils bound in a calcite cement and are smooth and flattish on one side and convex and convoluted on the other (the side shown here). 6, *Ctenothrissa* sp., $\times 6.7$; Bed 1, Merstham. 7, *Scapanorhynchus subulatus* (Agassiz), $\times 2$; Top Bed 1, Folkestone (locality 1). 8, *Trachyaster* cf. *rugosus* (Spencer), $\times 6.7$; Bed 1, Steyning.
- Figs. 9–15. Warm-water group (mainly Bed 2 and above). 9, *Entolium membranaceum* (Nilsson), $\times 2$; Bed 2, Eastbourne (locality 1). 10, '*Rhynchonella*' *lineolata* Phillips *carteri* Davidson, $\times 2.67$, somewhat crushed, *a* brachial valve aspect, *b* lateral aspect; Bed 2, Gogs Pit. 11, *Plicatula barroisi* Peron, $\times 2$; Bed 3, Merstham. 12, *Discoidea subuculus* Leske tr. *minima* Agassiz, $\times 2$; lower height and more rounded apex than in fig. 13; Top *subglobosus* Zone, Heacham. 13, *Discoidea minima* Agassiz, $\times 2$; Bed 4, Steyning. 14, *Cidaris perornata* Forbes, $\times 2$, fragment of spine; Bed 4, Winchester. 15, *C. hirudo* Sorignet, $\times 1.33$, spine, slightly abraded; Melbourn Rock, Merstham.
- Figs. 16–18. North Boreal group, with central European Russian affinities, mainly in Beds 4–6. 16, *Aequipecten arlesiensis* (Woods), $\times 2$; Bed 4, Steyning. 17, *Oxytoma seminudum* (Dames), $\times 2$, right valve; Bed 4, Folkestone (locality 1). 18, *Actinocamax plenus* (Blainville), $\times 0.67$; Bed 4, Folkestone (locality 1).
- Figs. 19–26. Aragonitic group; distribution controlled mainly by preservation, not ecology. 19, *Metoicoceras geslinianum* (d'Orbigny), $\times 0.67$; Bed 3, Merstham. 20, *Metoicoceras gourdoni* (Grossouvre), $\times 0.67$; Bed i, Cap d'Antifer. 21, *Cerithium* sp., $\times 2.67$; Bed i (= Bed 4), Crésantignes. 22, *Solarium* sp., $\times 2.67$; found inside a large ammonite, Bed 1, Crésantignes. 23, ? *Grammatodon* cf. *cenomanense* (d'Orbigny), $\times 2$; Bed 3, Merstham. 24, *Sciponoceras* sp., $\times 1$; Melbourn Rock, Merstham. 25, *Dentalium* sp., $\times 1.33$; Bed 7a, Eastbourne (locality 2). 26, *Aporrhais* sp., $\times 1.33$; Bed 3, Merstham.
- Figs. 27–32. Miscellaneous group; forms which do not belong to any of the previous groups, but which have stratigraphical importance or anomalous distribution. 27, *Ostrea vesicularis* Lamarck, $\times 2$; small form typical of the *subglobosus* Zone, with cast of turreted gastropod on attachment area; Top *subglobosus* Zone, Merstham. 28, *O. vesicularis* Lamarck, $\times 1.33$; large form typical of Beds 1 and 2; Bed 1, Merstham. 29, *Ditrupa difformis* (Lamarck), $\times 1.33$; Bed i (tourtia de Mons), Bellignies. 30, *Terebratulina* cf. *nodulosa* Etheridge, $\times 6.7$, pedicle valve aspect. 31, *Ornatothyris* sp., $\times 1.33$, *a* brachial valve aspect, *b* pedicle valve aspect; Base Bed 3, Marham. 32, *Orbirlhynchia wiesti* (Quenstedt), $\times 1.33$, *a* brachial valve aspect, *b* anterior aspect.



'Oyster-cast' preservation occurs when the aragonitic fossils are preserved merely as impressions on the attachment areas of *Ostrea vesicularis* (Pl. 77, fig. 27). Oyster casts, usually of small turreted gastropods, are found mainly in the top of the *subglobosus* Zone and Bed 1, in which aragonitic fossils of normal or pebble preservation are almost entirely absent and, together with the presence of the calcitic aptychi of ammonites, they prove that animals with aragonitic shells lived in the sea at the time of deposition of these beds but that their shells were later destroyed.

Distribution of normally preserved Aragonitic fossils. Normally preserved aragonitic fossils are distributed in England as shown in text-fig. 3. Their distribution in the thick sections of standard succession in the eastern Paris Basin (Crésantignes and Cernay-en-Dormois) is similar to that in the South Downs.

In the top of the *subglobosus* Zone and in Bed 1 normally preserved aragonitic fossils are usually rare (except in Bed 1 at Lulworth) although oyster casts are fairly common at these horizons. Normally preserved aragonitic fossils become much commoner at the base of Bed 2 over nearly the whole area of standard succession except near the Wash where the beds are thin (text-fig. 3); Krumbein and Sloss (1951, p. 421), using data from Pike (1947), have noticed a similar tendency for ammonites to be common in thick successions in the Cretaceous of New Mexico. Normal aragonitic fossils continue abundant in Bed 3 but they are rare in Beds 4–8 except when the *plenus* Subzone is more than about 10 feet thick as, for instance, at Eastbourne, Crésantignes, Steyning, Compton Bay (Isle of Wight), and Lulworth.

When the beds are thick and muddy, normally preserved fossils are usually limonitized, e.g. Eastbourne, Crésantignes, and Steyning. This limonitization, however, is probably the result of the recent conversion of marcasite or pyrite. This is suggested by the presence at Eastbourne of ammonites which are partly marcasite or pyrite and partly limonite, for these fossils doubtless owe their only partial conversion to the fact that Recent marine erosion is particularly strong at Eastbourne so that fossils have not long been near enough the surface of the ground to be subject to the action of oxygen-charged, percolating water.

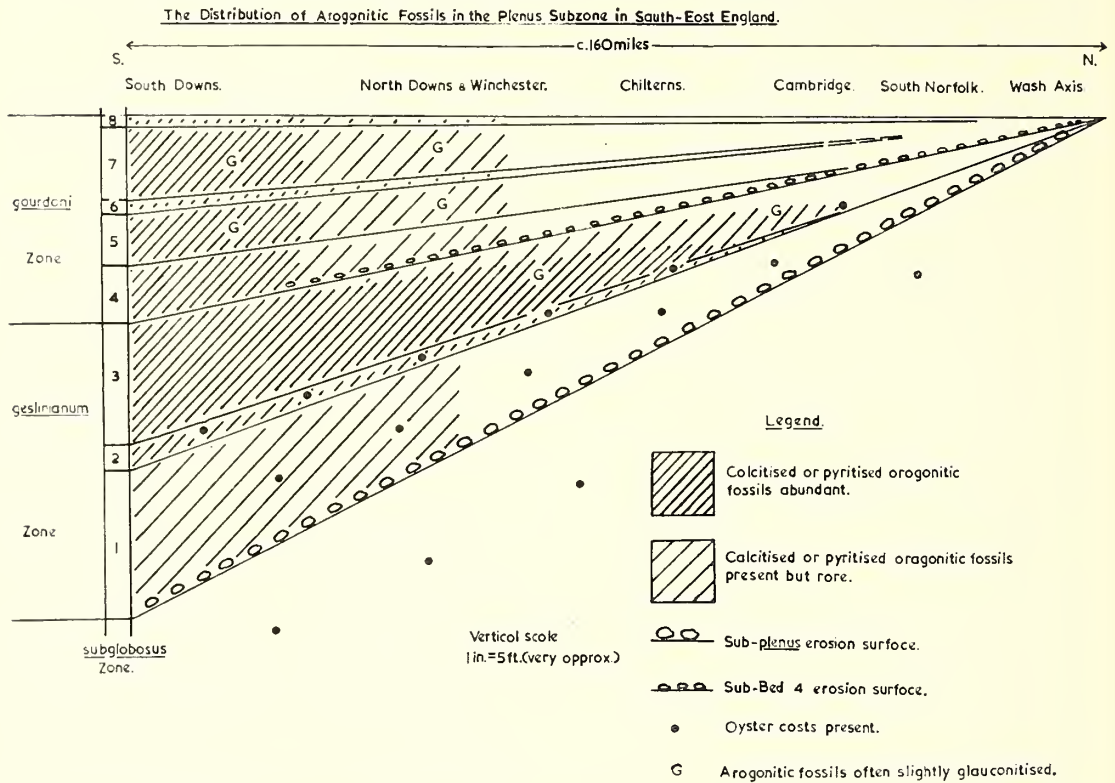
In any given bed the proportion of aragonitic fossils which are slightly glauconitized rises as the bed gets thinner. Thus at Merstham (Subzone 7 ft. 6 in. thick) many of the aragonitic fossils in Beds 2–3 and 3 and nearly all of those in Beds 4–8 are greenish. On the other hand, at Eastbourne (18–25 ft. thick) greenish aragonitic fossils are rare throughout the succession, though commoner in Beds 4–8 than below.

Normally preserved aragonitic fossils are especially common in or near large ammonites. This was noticed in the course of the present work in Bed 1 at Crésantignes (where a *Solarium* was found inside a large ammonite) and also in Beds 2–3 at Royston and Bed 2 at Steyning. The same phenomenon has been noticed by many writers in other beds of the Chalk (Godwin-Austen 1860, Lamplugh 1904, Wright and Wright 1942) and Davis (1926) similarly noted that aragonitic fossils were often found inside echinoids but not in the surrounding matrix.

Factors controlling the preservation of normal Aragonitic fossils. The distribution of normal aragonitic fossils in the *plenus* Subzone and top of the *subglobosus* Zone can largely be explained by variation in temperature (and therefore in CO₂ content of the

sea water), in turbulence of the bottom water, and in length of exposure on the sea-floor (which would be related to rate of deposition and indirectly to turbulence). Other probable, though less important, factors are the rate of pyritisation (or marcasitisation) or calcitisation and the initial strength, weight, and thickness of the shell.

The absence of aragonitic fossils from such beds as Bed 1 and the top of the *subglobosus*



TEXT-FIG. 3. The distribution of aragonitic fossils in the *plenus* Subzone in south-east England.

Zone is probably due to the fact that aragonite, but not calcite, was dissolved by the bottom water, which in this respect was comparable with the bottom water above *Globigerina* Ooze in Recent oceans; this, in turn, was probably connected with low temperature. The solubility of calcium carbonate in sea water has recently been discussed by Revelle and Fairbridge (1957, pp. 250 ff., esp. fig. 5). It appears that in surface sea water of normal salinity and alkalinity (Ca content) aragonite is always more soluble than calcite. A fall in temperature has two effects; it increases the solubility of aragonite or calcite (unlike most other solids) and also increases the solubility of atmospheric CO_2 which lowers the pH (though less than might be expected because of the buffer capacity of sea water). Consequently in equilibrium with an atmospheric partial pressure of about 3×10^{-4} atm. (the present-day value), and neglecting CO_2 produced by organisms, sea water in the laboratory will dissolve aragonite but not calcite at a temperature lower than 5°C .

In trying to apply these results to the Chalk one can presumably neglect the effect of great hydrostatic pressure which appreciably raises the apparent solubility product of both calcite and aragonite at depths of the order of 1,000 metres and also lowers the pH (Revelle and Fairbridge 1957, p. 254). The effect of the production of CO_2 by organisms in the water is more important, however. This is limited under aerobic conditions by the saturation volume of dissolved oxygen per litre (Revelle and Fairbridge 1957, p. 251). At 10°C . and 20‰ chlorinity this is 7.07 c.c./litre (Harvey 1955, table p. 184). Total respiration of this would produce the same volume of CO_2 which, from Revelle and Fairbridge (fig. 5), suggests that aragonite would just be dissolved given a partial atmospheric pressure of CO_2 of 3×10^{-4} atm. Consequently, on the simple though very uncertain assumption that Cretaceous sea water behaved like Recent sea water in this respect, Bed 1 and the top of the *subglobosus* Zone were deposited at a temperature lower than 5° or 10°C .

The widespread appearance of aragonitic fossils at the base of Bed 2, therefore, would suggest a rise in the temperature of the bottom water from below to above the equilibrium temperature of aragonite (which agrees with the change of the fauna towards a more shallow-water type). This level is thus comparable with the Chalk Marl, Chalk Rock, and Top Rock in which aragonitic fossils occur and which are usually regarded as shallow-water bands. By contrast, the southward retreat of aragonitic fossils at the base of Bed 4 may be connected with a decrease in temperature which is also suggested by the fauna. There is a possibility, however, that this southward retreat may also be partly due to an increase in turbulence as indicated by the sub-Bed 4 erosion surface.

Superimposed on the basic pattern connected with temperature is another pattern connected with turbulence and length of exposure on the sea bottom. Even at a period when the temperature of the bottom water was usually higher than the equilibrium temperature of aragonite, aragonitic fossils would still be expected to weaken quicker than calcitic ones because of chemical alteration (to pyrite, marcasite, or calcite) and also, perhaps, by intermittent solution caused by occasional lowering of the temperature below equilibrium for aragonite. This progressive weakening would gradually increase the likelihood that tumbling on the sea floor in turbulent bottom water would destroy the fossil. Consequently preservation of normal aragonitic fossils would be favoured, other things being equal, by rapid burial after death, by the absence of disinterments and by low turbulence in the bottom water during the periods when the fossil was in fact exposed. Areas of rapid and permanent burial would be areas of fast deposition and this explains why normal aragonitic fossils are commonest where the beds are thickest. Isolated points of low turbulence and permanent burial would be found in and underneath large ammonites which would themselves be protected from destruction by the thickness of their shells and their weight (which would prevent them being tumbled on the sea floor). This explains the frequent occurrence of aragonitic fossils in and around large ammonites. That the ammonites acted by producing sites of low turbulence rather than by somehow reducing solution rate is shown by the fact that in the Yorkshire Chalk Rock not only aragonitic fossils, but also certain types of calcitic ones, were preferentially preserved inside large ammonites (Wright and Wright 1942).

Distribution of Pebble preservation. Pebble preservation is commonest in condensed successions and fossils so preserved are older than their present matrix. Instances

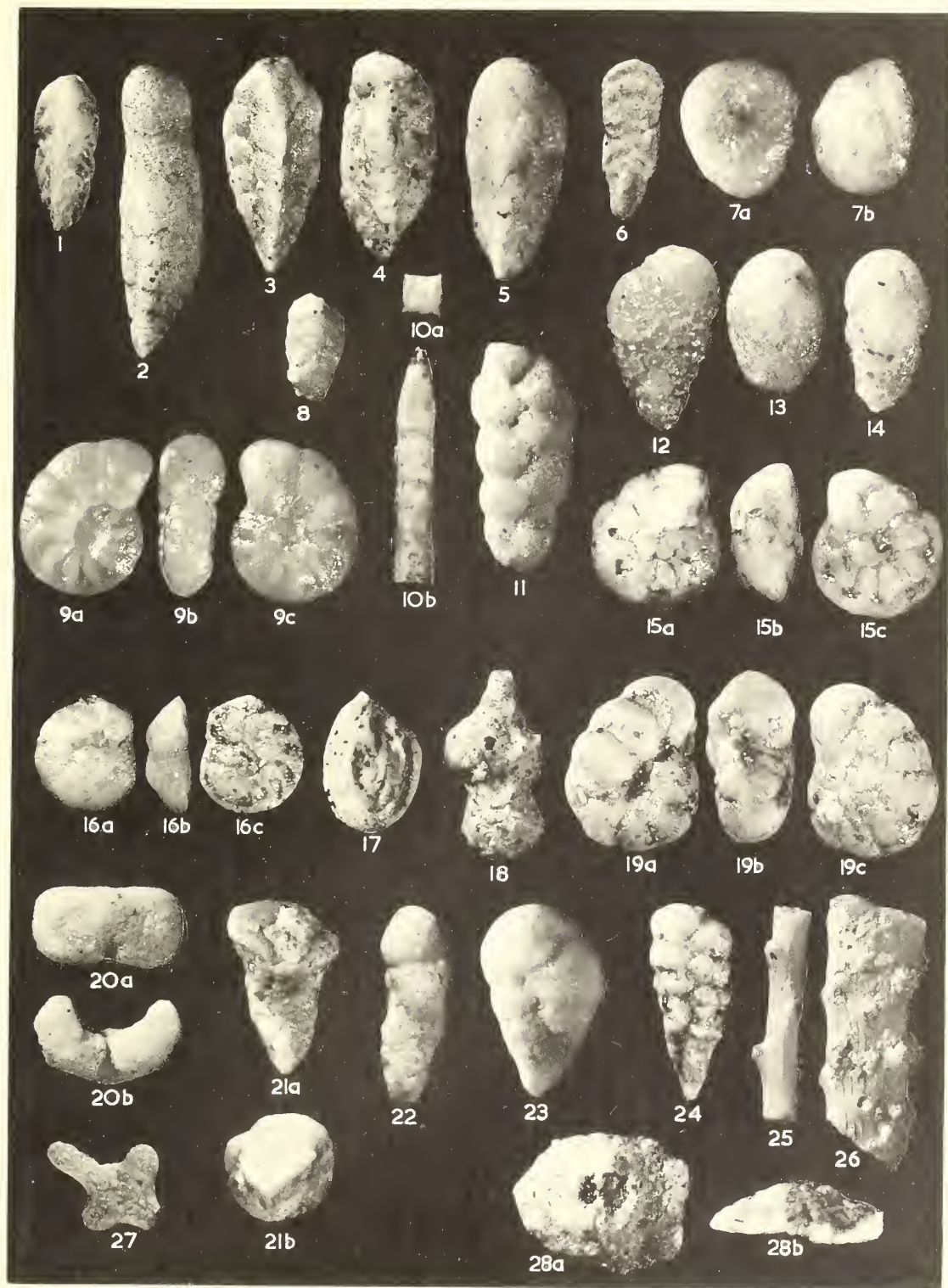
(Jefferies 1961) are the slightly phosphatized Cenomanian ammonites in Bed C at Hooken Cliff (Beer), the glauconitized ammonites at the base of the *labiatus* Zone at Haven Cliff, Seaton, the similar green-coated fossils at the base of the Turonian at Cap d'Antifer and Rouen and the phosphatized fossils at the base of the Turonian at Bellignies. There is also at least one case where pebble fossils occur in the standard succession (Bed 7, Eastbourne, loc. 2). In this instance the fossils are not glauconitized but covered with a patchy limonitic skin.

However, not all conglomerates of chalk pebbles associated with the *plenus* Subzone contain aragonitic pebble fossils. Thus there seem to be few or no such fossils in the conglomerate at the base of Bed 1 at any of the sections examined, or in the pebble bed (Bed 1) above the sub-*plenus* erosion surface at South Ferriby.

Factors controlling Pebble preservation. Turbulence and length of exposure prevented the preservation of normal aragonitic fossils in southern Norfolk and Cambridgeshire

EXPLANATION OF PLATE 78

- Figs. 1–15. Cold-water group; forms commonest in, and usually confined to, Bed 1 and the *subglobosus* Zone. 1, *Tristix excavatus* (Reuss), lateral aspect, $\times 40$; Pitstone, 0–3 in. below top *subglobosus* Zone. 2, *Tritaxia tricarinata* (Reuss) var. *plummerae* Cushman; one variety of a very variable species, lateral aspect, $\times 20$; Eastbourne (locality 4), Bed 1, 36 in. above base. 3, *T. tricarinata* (Reuss) var. *pyramidata* Reuss, lateral aspect, $\times 20$; Eastbourne (locality 4), Bed 1, 36 in. above base. 4, *T. tricarinata* (Reuss) var. *macfadyeni* Cushman, lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 4, 34 in. above base. 5, *T. tricarinata* (Reuss) var. *macfadyeni* Cushman, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 6, *Spiroplectinata* cf. *complanata* (Reuss), $\times 40$; form intermediate between *S. complanata* (Reuss) and *S. jaekeli* Franke; Eastbourne (locality 3), Bed 1, 0–3 in. above base. 7, *Pernerina* sp., *a* apertural aspect, *b* lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 8, *Spiroplectanmina* sp., lateral aspect, $\times 40$; Eastbourne (locality 3), 0–6 in. below top *subglobosus* Zone. 9, *Gavelinella baltica* Brotzen, *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 10, *Nodosaria prismatica* Reuss, *a* apertural, *b* lateral aspect, $\times 40$; Merstham, Bed 1, 0–3 in. above base. 11, *Dorothyia gradata* (Berthelin), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 12, *Plectina ruthenica* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 13, *Hagenowella advena* Cushman, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 12 in. above base. 14, *Verneuillina polystrophala* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 15, *Pseudovalvulineria* sp., *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base.
- Figs. 16–28. Warm-water group; forms which enter or increase at the base of Bed 2 in the area of standard succession. 16, *Cibicides* cf. *turonica* Brotzen, *a* spiral, *b* apertural, *c* umbilical aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 17, *Quinqueloculina antiqua* (Franke), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 18, *Reophax* sp., lateral aspect, $\times 20$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 19, *Anomalinoidea globosa* Brotzen, *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 20, asteroid terminal plate, *a* external aspect, *b* aspect showing slit for tube-foot, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 21, *Siphogaudryina* sp., *a* lateral aspect, *b* apical aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 22, *Gaudryina* sp., lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 23, *Textularia chapmani* Lalicker, lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 2, 12–14 in. above base Bed 1. 24, *Textularia* cf. *washitensis* Carsey, lateral aspect; the chambers are somewhat more inflated than in *T. washitensis*, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 25, *Siphoniotyphlus tenuis* (Hagenow), thin branch, $\times 20$; Eastbourne (locality 1), Bed 2, 34–36 in. above base Bed 1. 26, Thick branch of same $\times 20$. Same locality. 27, Star plate. Probably from the abactinal surface of *Calliderma smithiae* (Forbes), $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 28, *Marssonella* sp., *a* apical, *b* lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 2, 35–36 in. above base Bed 1.



where a somewhat reduced version of the standard succession is present. In Devon and the west Paris Basin, however, where the water was probably shallower, and where length of exposure and turbulence, as judged by net deposition, were greater, aragonitic shells were not destroyed but were preserved as pebble fossils. Obviously some factor other than turbulence must distinguish the two cases.

Rate of lithification was probably the factor involved and in the case of some pebble fossils at least, lithification seems to have happened fairly early. Thus *Metoicoceras* at the base of the Turonian at Haven Cliff, Seaton, is sometimes preserved as an almost perfect 'Steinkern'. This indicates that when the fossil was disinterred by erosion it retained its shape (though the shell had been broken away) because of the hardness of the chalk inside it. In other words, whereas a normal aragonitic fossil progressively weakened after death so that its chance of preservation was inversely proportional to length of exposure, a pebble fossil was strengthened shortly after death by the hardening of the chalk inside it. After this it would be almost indestructible, since, with further rolling on the sea floor, it would be hardened still further by phosphatization. Apart from being less strongly phosphatized, the pebble fossils of the *plenus* Subzone are thus very like the phosphate nodules of the Cambridge Greensand or of the Rouen Horizon which Cayeux (1939, p. 167, 184) regarded as phosphatized, reworked pebbles of chalk.

When pebble fossils are absent from conglomerates of chalk pebbles they were probably destroyed by solution, chemical changes, or mechanical action before they had a chance to be incorporated in the conglomerate. The occurrence in Bed 7 at Eastbourne probably points to the presence of a small erosion surface. The rapid lithification of shallow-water chalks may indicate the presence in the parent ooze of aragonite which, because of the high temperature of the bottom water, was converted to calcite cement instead of being dissolved (Black 1953, p. lxxv in discussion).

The author's views on the preservation of aragonitic fossils in the Chalk have been deeply influenced by those of Mr. M. Black, of Cambridge, as propounded in lectures and discussion. The author would like to express his gratitude to Mr. Black, though the opinions expressed are naturally his own responsibility.

METHODS USED IN STUDYING FAUNAL DISTRIBUTION

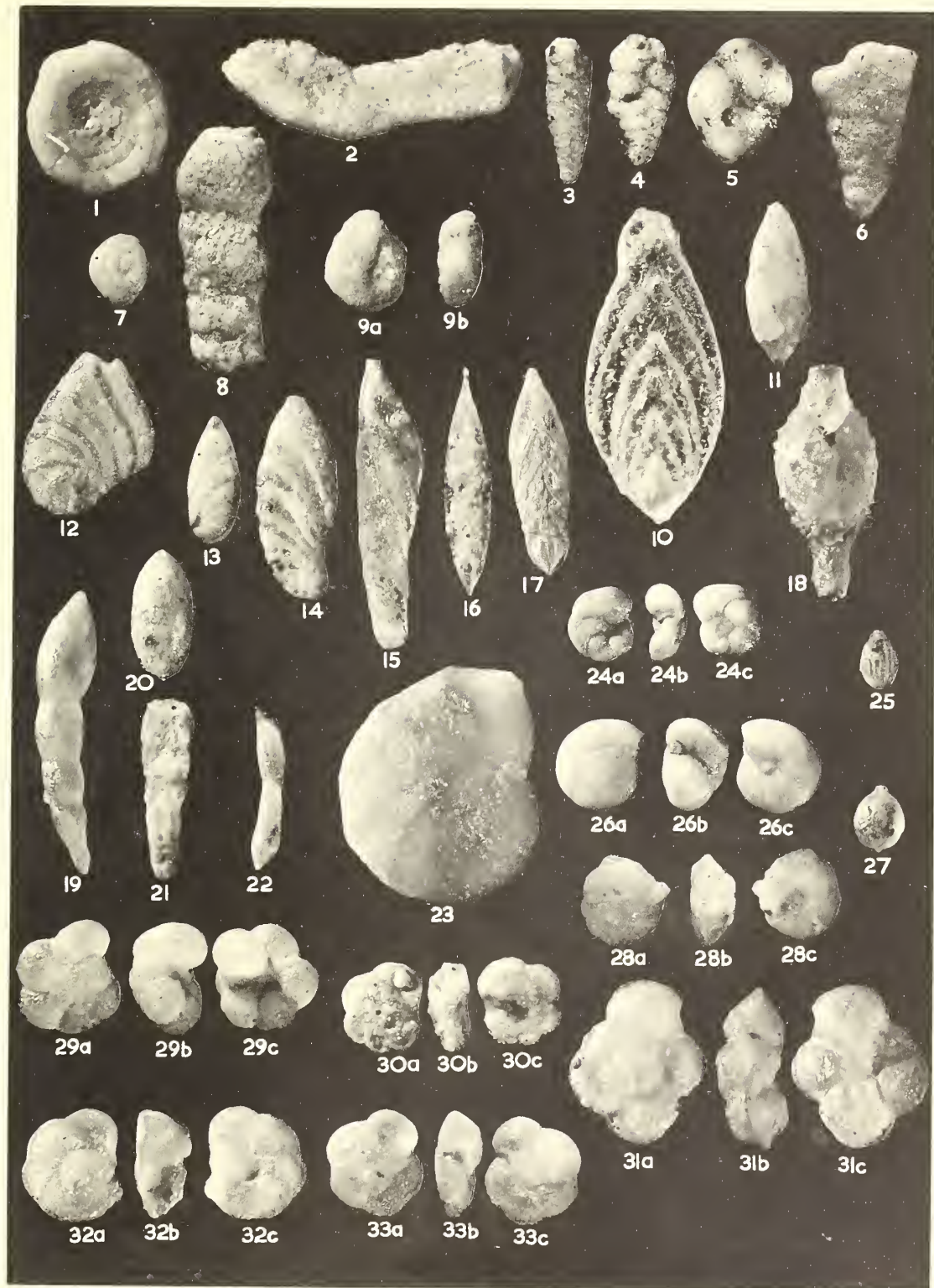
The study of the palaeoecology of the *plenus* Subzone and the top of the *subglobosus* Zone was based partly on the macro- and partly on the microfauna and partly on general considerations such as the gross lithology of the rocks, their position in the Anglo-Paris Basin, the presence of erosion surfaces and whether or not aragonitic fossils were preserved. The distribution of the macrofossils was studied by bed-by-bed collecting at some forty localities in the Anglo-Paris Basin (Jefferies 1961). The microfossils, on the other hand, were studied by extracting them from the rock and counting them. The results of counting are shown in the form of distribution graphs in text-figs. 4-11.

The method used for extracting the microfauna was as follows: the sample was broken into pieces about $\frac{1}{2}$ in. across and prominent burrows were removed. A known volume (up to 200 c.c.) of these pieces was then immersed in water in a jam jar and broken down by repeated freezing and thawing. Any pieces which would not pass a 5-mm. sieve after this treatment were crushed with a pestle and mortar and returned to the sample. This was then placed in a 3-lb. Kilner jar, topped up to 750 c.c. with water and shaken on a shaking machine for three to four hours at about 70 cycles/min. The resulting sludge

was thinned out by wet-sieving through a 200-mesh sieve and the portion retained by the sieve was returned to the Kilner, topped up to 750 c.c. again and shaken for a further three to four hours to clean the microfossils. Sometimes, when the rock was hard, two to four 1- or 1½-inch rubber bungs were placed in the Kilner during the shakings to act as mill balls. After a second shaking the sample was wet-sieved again through a 200-mesh sieve, dried on the sieve over a radiator, and dry-sieved through an 80-mesh sieve. The fractions passed and retained by the 80-mesh sieve were then ready for storage unless the coarse fraction contained many large fragments, in which case it was dry-sieved through a 30-mesh sieve and any microfossils in the 30-mesh fraction were picked out and added to the 80-mesh fraction before the latter was stored.

EXPLANATION OF PLATE 79

- Figs. 1–28. Miscellaneous group; benthonic Foraminifera which do not belong to either the cold- or the warm-water behaviour groups. 1, *Ammodiscus cretaceus* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 3, 34–36 in. above base Bed 1. 2, ?*Rhizammina algaeformis* Brady; a rare species included with *Ramulina aculeata* in the counts, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 3, *Gaudryina foeda* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 4, *G. serrata* Franke, lateral aspect, $\times 40$; Bellignies, Bed iv, 0–2 in. above base. 5, *Eggerellina* sp., lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 6, *Marssonella trochus* (d'Orbigny), lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 1, 1–20 in. above base. 7, *Glomospira charoides* (Parker and Jones) var. *corona* Cushman and Jarvis, $\times 40$; Bellignies, Bed ii, 2–6 in. above base. 8, *Bulbophragminium* sp., fragment of uniserial portion, $\times 20$; Eastbourne (locality 4), Bed 1, 12 in. above base. 9, *Haplophragmoides latidorsatum* (Bornemann), *a* lateral, *b* apertural aspect, $\times 40$; Merstham, Bed 4, 0–4 in. above base. 10, *Frondicularia bicornis* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 11, *Globulina prisca* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 12, *Palmula elliptica* (Nilsson), lateral aspect of juvenile specimen, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 13, *Vaginulina complanata* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 6. 14, *V. parallela* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 2), Bed 4, 17–20 in. above base. 15, *V. costulata* (Römer), lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 16, *Frondicularia inversa* Reuss; not separated from *F. solea* in the counts, $\times 40$; Eastbourne (locality 2), Bed 4, 3–6 in. above base. 17, *F. solea* Reuss; not separated from *F. inversa* in the counts, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 18, *Ramulina aculeata* Wright, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 19, *Dentalina* sp., lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 20, *Pseudoglandulina concinna* (Reuss), lateral aspect, $\times 40$; Eastbourne (locality 3), Bed 1, 0–2 in. above base. 21, *Nodosaria raphanus* (Linne) *obscura* Reuss, lateral aspect, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 22, *Dentalina filiformis* (Reuss), lateral aspect, $\times 40$; Briollay, Sarthe, 'marnes à ostracées'. 23, *Lenticulina rotulata* Lamarck, lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 24, *Discorbis allomorphinoides* (Reuss), *a* umbilical, *b* apertural, *c* spiral aspect, $\times 40$; Briollay, Sarthe, 'marnes à ostracées'. 25, *Lagena multistriata* Marsson; possibly an *Entosolenia*; lateral aspect, $\times 40$; Briollay, Sarthe, 'marnes à ostracées'. 26, *Gyroidinoides nitida* (Reuss), *a* spiral, *b* apertural, *c* umbilical aspects, $\times 40$; Pitstone, *subglobosus* Zone, 0–3 in. below top. 27, *Entosolenia* sp., lateral aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 36 in. above base. 28, *Cibicides formosa* Brotzen, *a* spiral, *b* peripheral, *c* umbilical aspects, $\times 40$; Merstham, Bed 7a.
- Figs. 29–33. Planktonic Foraminifera. 29, *Globigerina portsmouthensis* Williams–Mitchell; commonest member of the Globigerinidae in the *plenus* Subzone; *a* spiral, *b* apertural, *c* umbilical aspects, $\times 40$; Eastbourne (locality 1), Bed 2, 17–20 in. above base Bed 1. 30, *Globotruncana lapparenti* Brotzen *lapparenti* Brotzen, *a* spiral, *b* apertural, *c* umbilical aspect, $\times 40$; Bellignies, 0–2 in. above base. 31, *Rotalipora turonica* (Brotzen), *a* spiral, *b* peripheral, *c* umbilical aspect, $\times 40$; Eastbourne (locality 4), Bed 2, 0–2 in. above base. 32, *Thalmanninella deeckei* (Franke), *a* spiral, *b* apertural, *c* umbilical aspect, $\times 40$; Eastbourne (locality 4), Bed 1, 68 in. above base. 33, *Praeglobotruncana* sp., *a* spiral, *b* apertural, *c* umbilical aspects, $\times 40$; Eastbourne (locality 2), Bed 4, 9–12 in. above base.



This method of extraction is based on a method used by Burnaby on the Chalk Marl (Burnaby 1961). The modification of Burnaby's method for use on the *plenus* Subzone (which includes harder rocks than the Chalk Marl) took several months so that the early extractions (at Eastbourne and Merstham) were less successful than the later ones (Pitstone and Crésantignes). This is shown by the average number of benthonic foraminifera large enough to be retained by an 80-mesh sieve which were extracted per c.c. of rock (Merstham 32.2, Eastbourne 40.8, Pitstone 71.6, Crésantignes 78.5). However, ecological interpretation is based mainly on the percentage composition of the microbenthos so that destruction is only important in so far as it affects some species more than others. The good agreement in the distribution graphs of Merstham (text-fig. 6) with Pitstone (text-fig. 7), on the one hand, and of Eastbourne (text-fig. 8) with Crésantignes (text-fig. 10) on the other, suggests that percentage destruction was largely uniform as between the different species of microbenthos and can therefore be disregarded.

Taxonomic examination was carried out on a half of each prepared sample from Eastbourne, the samples having been halved on a Burnaby rotary sample splitter. Any new species which appeared during the counting of later samples were transferred to a special miscellaneous taxonomic slide for later study. The foraminifera encountered are figured in Plates 78–79.

Counting was by a two-order procedure also developed by Burnaby; only the material large enough to be retained by an 80-mesh sieve (0.2 mm.) was counted. For the first-order count this was divided on a Burnaby sample splitter into fractions guessed to contain less than about 100 microfossils. Using a squared microfossil slide as a counting tray and a previously prepared tally sheet for recording, enough of these fractions were then counted completely for a total of more than 300 microfossils to be reached. The material which had been scanned was then weighed and the tally sheet examined to see which species had reached a total of eight or more. These constituted the first-order species. The second-order count proceeded like the first-order count except that specimens of first-order species were not recorded. Counting continued until the number of specimens of second-order species (those which had reached seven or less in the first-order count) also exceeded 300. When the second-order count was complete all the material which had been scanned (both orders) was weighed. The number of specimens of a first-order species which would have been counted if counting had continued can be estimated from the equation:

$$N = \frac{nW_2}{W_1}.$$

Where N is the estimate, n the recorded number in the first-order count, W_1 the weight of the first-order material, and W_2 the weight of first- and second-order material. From the observed and estimated frequencies the per mil. frequencies of the different species can easily be calculated. The advantage of a multi-order counting method is that a reasonable number of specimens of a rare species can be counted without counting an enormous number of a common one. This is particularly useful for counting mixed plankton and benthos since the plankton is normally much commoner and has fewer species than the benthos.

The distribution diagrams are constructed on the following basis: Benthonic

foraminifera + bryozoa + asteroid ossicles = $B = 1,000$. Ostracods (one group only) and *Roveacrinus* ossicles are plotted on the basis $B = 1,000$. Planktonic foraminifera = $P = 1,000$. The justification for this method of plotting the results is that plankton is more abundant than benthos so that numerical variation in the plankton would obscure per mil. variation in the benthos, and that plankton and benthos represent separate communities which for ecological purposes should be treated separately.

THE UPPER PART OF THE SUBGLOBOSUS ZONE

The macrofauna of the upper *subglobosus* Zone is rather meagre in the area of standard succession, but many of the groups which are rare or absent in this area can be found nearer the edges of the Anglo-Paris Basin in Norfolk, Yorkshire, and Lincolnshire, or at Cap d'Antifer.

The fauna of the area of standard succession includes *Scapanorhynchus subulatus*, small turreted gastropods (as oyster casts only), *Schloenbachia* sp. (limonitized specimen at Crésantignes), *Plicatula inflata*, *P. barroisi*, *Entolium orbiculare*, *Aequipecten beaveri*, *Neitheia quinquecostata* (c), *Inoceramus pictus* (c), *Ostrea vesicularis* (small form) (c), *Lingula* sp. (c), *Terebratulina striatula* (c), *T.* cf. *nodulosa*, *Holaster trecensis* (c), 'problematicum' (c). Serpulids, Rhynchonellids, Terebratulids (except *Terebratulina*), asteroids, Cidarids, bryozoa, and the group of small *Discoidea* (represented at this level by *D. subuculus*) are possibly absent and certainly very rare. In this and subsequent lists (c) indicates common.

Westwards, however, at Cap d'Antifer, the top of the *subglobosus* Zone contains the Rhynchonellids *Orbirhynchia multicostata*, *O. compta*, and *O.* cf. *cuvieri* (the first of these being the commonest macrofossil), *Discoidea subuculus* and fragments of large bryozoa. Northwards the Terebratulid *Ornatothyris sulcifera* and also spines of *Cidaris hirudo* are common in a nodular band 20 feet below the top of the *subglobosus* Zone at Cherry Hinton. Furthermore, in northern Norfolk and Lincolnshire the Terebratulids *Concinuithyris burhamensis* and *C. subundata*, perhaps the same species (at Heacham, Hillington, and South Ferriby) and also *Discoidea subuculus* (at Heacham) and *Cidaris perornata* (at Heacham) occur in the top of the *subglobosus* Zone.

In explaining this faunal variation possible chronological differences cannot be left out of account. The *plenus* Subzone is condensed or absent in northern Norfolk, Lincolnshire, and Cap d'Antifer suggesting that some feet of chalk at the top of the *subglobosus* Zone may also be missing. It seems unlikely, however, that this possible age difference entirely accounts for the faunal differences, since the Rouen Horizon (early *subglobosus* Zone) is 35 feet below the top of the Zone at Cap d'Antifer and the Lower Chalk of Norfolk seems condensed rather than incomplete (Jukes-Browne and Hill 1903, fig. 2, p. 23). Much the most likely explanation of the peripheral distribution of these groups, therefore, is that Norfolk and Lincolnshire on the one hand, and Cap d'Antifer, on the other, were shallow-water areas on either side of the Weald and Central Paris Basin. Shallow water at Cap d'Antifer is suggested by the presence in the Cenomanian of numerous erosion surfaces and glauconitic bands and in Norfolk by the thinness of the Cenomanian and its lack of mud.

The softness of the bottom in the area of standard succession was probably responsible for the absence there of Rhynchonellids and most Terebratulids. This is suggested by the

fact that the two types of brachiopods which do occur probably did not require hard bottom. Thus *Lingula* sp. probably lived in a burrow, held in place by the weight and mucous covering of its pedicle (Craig 1952, p. 112), and *Terebratulina*, by analogy with its Recent relative *Clidonophora* (cf. Elliott 1938, p. 129), may well have been able to anchor itself in soft ooze by means of a tuft of rootlet-like fibres on the end of its pedicle.

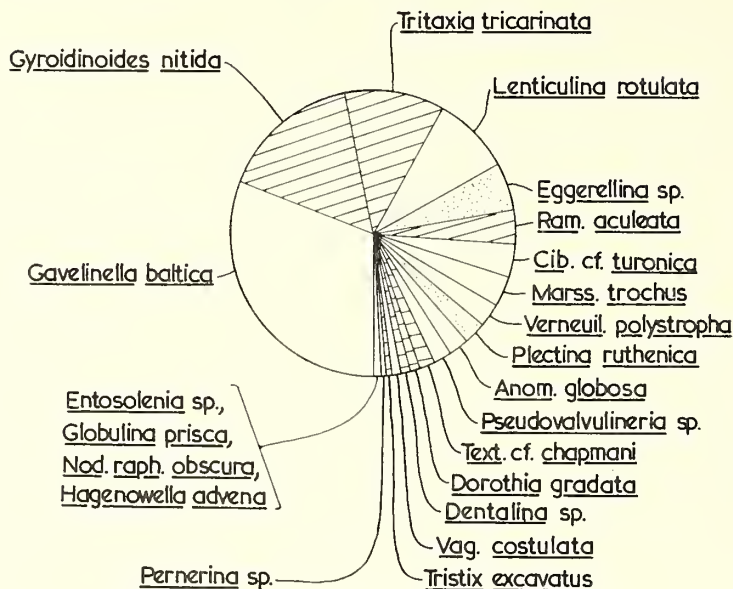
The microfauna confirms that the water at Cap d'Antifer was shallower than that of the area of standard succession. The composition of the benthonic microfauna of the latter is represented in text-fig. 4 by the pie-chart of sample 112 (top *subglobosus* Zone, Pitstone). It is very different from the benthonic fauna of sample 108 (top *subglobosus* Zone, Cap d'Antifer) and these differences are illuminating when compared with results from the *varians* Zone (from Burnaby 1961):

Name of species	Burnaby's nearest species	Depth preferred in <i>varians</i> Zone
Species commoner at Pitstone than at Cap d'Antifer		
<i>Gavelinella baltica</i>	<i>G. baltica</i>	neutral
<i>Gyroidinoides nitida</i>	<i>G. nitida</i>	deep
<i>Tritaxia tricarinata</i>	<i>T. pyramidata</i>	deep
<i>Ramulina aculeata</i>	<i>Ramulina</i> sp. A	deep
<i>Verneuilina polystrophia</i>	—	—
<i>Textularia chapmani</i>	<i>T. chapmani</i>	deep
<i>Dorothia gradata</i>	<i>D. gradata</i>	deep
<i>Dentalina</i> sp.	<i>Dentalina</i> sp.	deep
<i>Vaginulina costulata</i>	<i>Vaginulina</i> sp.	? neutral
<i>Tristix excavatus</i>	<i>T. excavatus</i>	deep
<i>Pernerina</i> sp.	—	—
Species commoner at Cap d'Antifer than at Pitstone		
<i>Plectina ruthenica</i>	<i>P. ruthenica</i>	shallow
<i>Cibicides</i> cf. <i>turonica</i>	<i>C.</i> cf. <i>sandidgei</i>	neutral
<i>Eggerellina</i> sp.	<i>Ataxophragmium compactum</i>	shallow
<i>Marssonella trochus</i>	<i>M. oxycona</i>	neutral
<i>Anomalinoidea globosa</i>	—	—
<i>Hagenowella advena</i>	<i>H. anglica</i>	shallow
Species equally common at both localities		
<i>Lenticulina rotulata</i>	<i>L. rotulata</i>	neutral

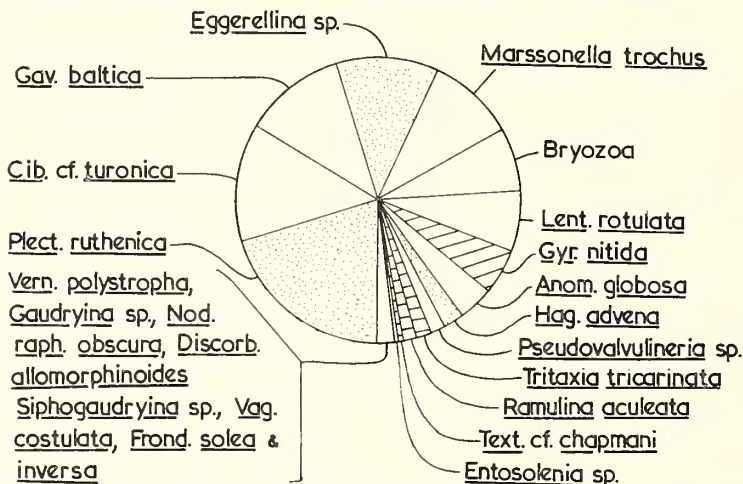
In drawing up the above table it has been assumed that species with their maximum in the middle of the *varians* Zone preferred deep water, that those with maxima at top and bottom preferred shallow water and that other species were neutral (Burnaby 1961). It is clear that species with deep-water relatives in the *varians* Zone were commoner at Pitstone than Cap d'Antifer and species with shallow-water relatives were commoner at Cap d'Antifer than at Pitstone.

Among the rarest species in the Cap d'Antifer pie-chart are two, *Gaudryina* sp. and *Siphogaudryina* sp., which became abundant in the standard succession at the base of Bed 2. These species are so rare in sample 108, however, that they might have been brought down by burrows from the *plenus* Subzone. But if indigenous to the *subglobosus* Zone they would suggest that the populations of these species in the *plenus* Subzone were descended, at least in part, from ancestors that lived in the area of Cap d'Antifer.

Sample 112, Pitstone, 0-3 ins. below top subglobosus Zone.



Sample 108, Cap d'Antifer, 9-12 ins. below top subglobosus Zone.



TEXT-FIG. 4. The constitution of the microbenthos in the topmost *subglobosus* Zone at Pitstone and Cap d'Antifer. Cross-hatched species have deep-water relatives and stippled species have shallow-water relatives in the *varians* Zone at Barrington (cf. Burnaby 1961).

The bryozoa at Cap d'Antifer are ill-preserved but probably do not include *Siphonotyphlus tenuis* which is the main species of the standard succession (in which it only occurs above Bed 1). Nevertheless, the fact that bryozoa were present in shallow water in late *subglobosus* times but not in deep water suggests that the bryozoa of the *plenus*

Subzone of the area of standard succession had ancestors living in areas of shallow water in *subglobosus* times.

THE PLENUS SUBZONE

Bed 1. The fauna of Bed 1 is very like that at the top of the *subglobosus* Zone. Such changes as do occur can partly be explained by shallowing and increase in mud content; they seem, however, significantly small in view of great lithological signs of shallowing (erosion and increased mud content) at the base of the bed.

The following species of macrofossils have been found in Bed 1: *Ctenothrissa* sp. (c), *Scapanorhynchus raphiodon*, *S. subulatus* (c), *Ptychodus decurrens*, *Calycoceras* sp., *Metoicoceras geslinianum* (as oyster casts), *Spondylus latus*, *Plicatula barroisi*, *Entolium membranaceum* (near top only), *E. orbiculare*, *Aequipecten beaveri*, *Neithea quinquecostata*, *Lima globosa*, *Teredo amphisbaena*, *Inoceramus pictus* (c), *Ostrea vesicularis* (large grypheate form) (c), *Liugula* sp. (c), 'Rhynchonella' *lineolata carteri*, *Orbirhynchia multicostata* (c), *Terebratulina striatula*, *T. cf. nodulosa*, *Cretiscalpellum glabrum*, *Enoploclytia* sp., ophiuroid, *Calliderma smithiae*, *Crateraster quinqueloba*, *Staurasteraster* sp., *Trachyaster* cf. *rugosus*, *Holaster trecensis*, *Micrabacia coronula* (? derived), 'problematicum' (c).

The changes at the base of Bed 1 may thus be summarized as follows: (i) *Plicatula inflata* and *Discoidea cylindrica* seem to have become extinct; (ii) *Holaster trecensis* is much rarer; (iii) certain species which are very rare or perhaps completely absent in the top of the *subglobosus* Zone of the area of standard succession appear or become much commoner. These include *Orbirhynchia multicostata* (c), 'Rhynchonella' *lineolata carteri* (rare), *Calliderma smithiae* (rare), *Trachyaster* cf. *rugosus*, *Metoicoceras geslinianum* (rare), and *Scapanorhynchus raphiodon*; (iv) two species which are definitely present in the *subglobosus* Zone become much commoner, *Ctenothrissa* sp. and *Scapanorhynchus subulatus*; (v) two species increase in average size, *Ostrea vesicularis* and *Neithea quinquecostata*.

The abundant *Orbirhynchia multicostata* in the area of standard succession in Bed 1 were probably in part descended from ancestors which lived in the Cap d'Antifer region in late *subglobosus* Zone times and their spread must almost certainly be due to shallowing. The same shallowing probably also accounts for the rare appearance in Bed 1 of certain species which become common at the base of Bed 2. This includes 'Rhynchonella' *lineolata carteri* and the asteroids *Calliderma smithiae* and *Crateraster quinqueloba*. Another asteroid, *Trachyaster* cf. *rugosus*, may also owe its appearance to shallowing though it became extinct at the base of Bed 2.

Changes connected with increased muddiness probably included the decline of *Holaster trecensis* and extinction of *Discoidea cylindrica* (since echinoids tend to dislike mud), and the increase in size of *Ostrea vesicularis* and *Neithea quinquecostata* due to increased food supply.

Normal aragonitic fossils, as pointed out above, are as rare in Bed 1 as in the *subglobosus* Zone except at Lulworth (Jefferies 1961), though oyster casts occur. This suggests that the pre-Bed 1 shallowing, though it produced a great increase in turbulence of bottom water and mud supply, caused no great rise in temperature. The absence of such a rise would explain why the faunal changes are so small.

The changes in the benthonic foraminifera, which are also slight, are summarized in the following table, based on Pitstone and Merstham (text-figs. 6, 7).

<i>Name of species</i>	<i>Behaviour in top subglobosus Zone</i>	<i>Burnaby's nearest sp.</i>	<i>Behaviour in varians Zone</i>
Species which disappears at the base of Bed 1			
<i>Tristix excavatus</i>	deep	<i>T. excavatus</i>	deep
Species which decrease at the base of Bed 1			
<i>Verneuilina polystropha</i>	deep	—	—
<i>Gyroidinoides nitida</i>	deep	<i>G. nitida</i>	deep
<i>Marssonella trochus</i>	shallow	<i>M. oxycona</i>	shallow
<i>Lenticulina rotulata</i>	neutral	<i>L. rotulata</i>	neutral
<i>Entosolenia sp.</i>	?	<i>Lagena A</i>	?
Species which increase or appear at the base of Bed 1			
<i>Tritaxia tricarinata</i>	deep	<i>T. pyramidata</i>	deep
<i>Plectina ruthenica</i>	shallow	<i>P. ruthenica</i>	shallow
<i>Hagenowella advena</i>	shallow	<i>H. anglica</i>	shallow
<i>Pseudovalvulineria sp.</i>	shallow	—	—
<i>Spiroplectinata cf. complanata</i>	—	<i>S. complanata</i>	bottom half
<i>Textularia cf. washitensis</i>	—	<i>T. subconica</i>	deep
Spp. which do not change in abundance at the base of Bed 1 or behave inconsistently from place to place			
<i>Pernerina sp.</i>	deep	—	—
<i>Gavelinella baltica</i>	deep	<i>G. baltica</i>	neutral
<i>Ramulina aculeata</i>	deep	<i>Ramulina A</i>	deep
<i>Dentalina sp.</i>	deep	<i>Dentalina sp.</i>	deep
<i>Anomalinoidea globosa</i>	shallow	—	—
<i>Cibicides cf. turonica</i>	shallow	<i>Cibicides cf. sandidgei</i>	neutral
<i>Eggerellina sp.</i>	shallow	<i>Ataxophragmium compactum</i>	shallow
<i>Textularia chapmani</i>	deep	<i>T. chapmani</i>	deep

Thus, among the species which show consistent change in abundance at both localities *T. excavatus* (extinction), *G. nitida* (decrease), *P. ruthenica* (increase), *Hagenowella advena* (increase), *Pseudovalvulineria* (increase) and *V. polystropha* (decrease) behave as would be expected from their distributions in the top *subglobosus* and *variens* Zones, assuming that the change at the base of Bed 1 was a simple shallowing. However, the deep-water *Tritaxia tricarinata* increased and the shallow-water *Marssonella trochus* decreased, and this perhaps suggests respectively a liking and a dislike for mud. Mud may also have influenced the size of the increase in *Pseudovalvulineria sp.* When this table is compared with the previous one it is clear that the change at the base of Bed 1 had less ecological effect than the difference between Pitstone and Cap d'Antifer in late *subglobosus* times.

Bed 2. Unlike the change at the base of Bed 1, the faunal change at the base of Bed 2 seems disproportionately large compared with any changes in lithology, which consist merely of an increase in mud content and certain signs of slower sedimentation or slight erosion (Jefferies 1961). In the macrofauna the changes are as follows: (i) A group of forms disappeared at least temporarily. These included *Ctenothrissa sp.*, *Scapanorhynchus subulatus* (except a single specimen in Bed 2–3 at Lulworth), *Neitheia quinquecostata*,

Lima globosa, *Lingula* sp., *Orbiryhynchia multcostata* (except for one specimen in Bed 2 at Steyning), *Cretiscalpellum glabrum*, *Trachyaster* cf. *rugosus*, 'problematicum', *Holaster trecensis* (except rare occurrences in Beds 5–7). This list includes nearly all the commonest species in Bed 1. (ii) Several macrofossils appear or become much commoner at the base of Bed 2: *Plicatula barroisi*, *Entolium membranaceum* (which occurs in Bed 1 only as a rarity near the top but which is the commonest fossil in Bed 2), *Cidaris perornata*, *C. hirudo*, *Discoidea minima*, *Calliderma smithiae* (c.), 'Rhynchonella' *lineolata carteri* (c.), *Scaphites equalis*, *Nucula* sp., *Solarium* sp., *Cerithium* sp., *Metoicoceras geslinianum*, *Protocardia hillana*, *Grammatodon* cf. *cenomanense*, *Aporrhais* sp., *Dentalium* sp. It is noteworthy that all the members of this group after '*R.*' *lineolata carteri* are aragonitic.

In the benthonic microfauna the changes can be expressed in tabular form (on the basis of text-figs. 6–10):

Name of species	Behaviour in subglobosus Zone	Burnaby's nearest species	Behaviour in varians Zone
Species which disappear at the base of Bed 2 and do not reappear in the rest of the Subzone			
<i>Verneuilina polystropha</i>	deep	—	—
<i>Plectina ruthenica</i>	shallow	<i>P. ruthenica</i>	shallow
<i>Pernerina</i> sp.	deep	—	—
<i>Dorothia gradata</i>	deep	<i>D. gradata</i>	deep
<i>Spiroplectinata</i> cf. <i>complanata</i>	—	<i>S. complanata</i>	bottom half
<i>Hagenowella advena</i>	shallow	<i>H. anglica</i>	shallow
<i>Gavelinella baltica</i>	deep	<i>G. baltica</i>	neutral
<i>Pseudovalvulineria</i> sp.	shallow	—	—
Species which disappears at the base of Bed 2 but which reappears in some places at the top of Bed 4			
<i>Tritaxia tricarinata</i>	deep	<i>T. pyramidata</i>	deep
Species which disappear or decline at the base of Bed 2 but which reappear or become common again in Bed 2 or the base of Bed 3			
<i>Gyroidinoides nitida</i>	deep	<i>G. nitida</i>	deep
<i>Marssonella trochus</i>	shallow	<i>M. oxycona</i>	neutral
<i>Ramulina aculeata</i>	deep	<i>Ramulina</i> sp. A	deep
<i>Ammodiscus cretaceus</i>	—	<i>Ammodiscus</i> sp.	deep
<i>Dentalina</i> sp.	deep	<i>Dentalina</i> sp. A	deep
<i>Lenticulina rotulata</i>	neutral	<i>L. rotulata</i>	neutral
Species present in Bed 1 which become much commoner in Bed 2			
<i>Anomalinoidea globosa</i>	shallow	—	—
<i>Cibicides</i> cf. <i>turonica</i>	shallow	<i>C.</i> cf. <i>sandidgei</i>	neutral
<i>Eggerellina</i> sp.	shallow	<i>Ataxophragmium compactum</i>	shallow
<i>Textularia chapmani</i>	deep	<i>T. chapmani</i>	? deep
<i>Textularia</i> cf. <i>washitensis</i>	—	<i>T. subconica</i>	deep
Asteroid terminals	shallow	—	—
<i>Quinqueloculina antiqua</i>	—	<i>Quinqueloculina</i> sp.	bottom half
Species which are absent in Bed 1 and the top of the subglobosus Zone in area of standard succession and which first occur in Bed 2			
<i>Siphogaudryina</i> sp.	? shallow	<i>Siphogaudryina</i> sp.	bottom half
<i>Reophax</i> sp.	—	—	—

Name of species	Behaviour in subglobosus Zone	Burnaby's nearest species	Behaviour in varians Zone
<i>Siphoniotyphlus tenuis</i>	—	—	—
<i>Gaudryina</i> sp.	? shallow	—	—
<i>Marssonella</i> sp.	—	—	—
Star plates	—	—	—

Notes. (1) The occurrence of *Verneuilina polystropha* in Bed 4 at Pitstone (text-fig. 7) is based on one specimen and is probably due to sieve contamination. (2) *Eggerellina* sp. increases at the base of Bed 2 at Crésantignes and Eastbourne but at Pitstone and Merstham does not increase till later. (3) *Quinqueloculina antiqua* was found in Bed 2 at Eastbourne and Crésantignes but not at Merstham or Pitstone; it was found in Bed 1 only at Eastbourne during taxonomic examination, but not during counting, and therefore does not appear in the distribution charts in that bed.

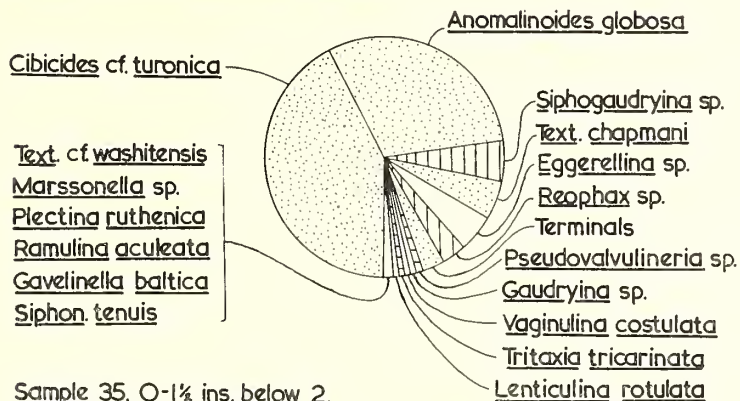
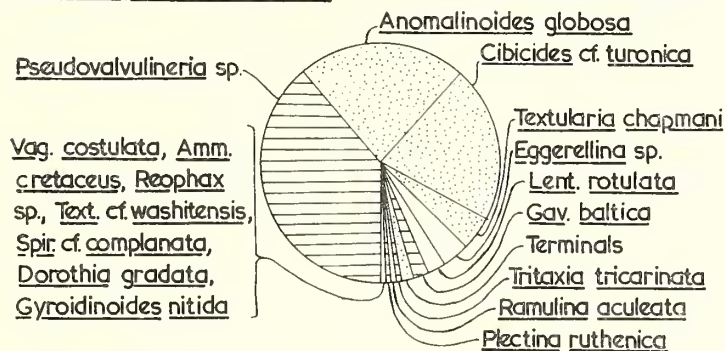
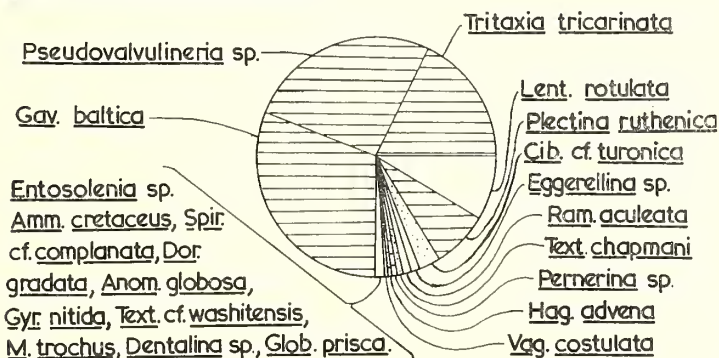
The main changes in the planktonic fauna are (again on the basis of text-figs. 6–10): (i) The extinction of *Thalmaninella deeckei*; (ii) An increase in *Praeglobotruncana* sp. This sometimes begins below the top of Bed 1 and sometimes the species declines for an interval shortly above the base of Bed 2 as at Crésantignes and Merstham. (iii) A decline in *Rotalipora turonica*. (iv) Generally an increase in Globigerinidae. (v) There also seems to have been an increase in the crinoid *Roveacrinus*.

The change at the base of Bed 2 seems to have started below the top of Bed 1. In the macrofauna this is indicated by a specimen of *Entolium membranaceum* just below the top of Bed 1 at Steyning. In the microbenthos the same thing shows more clearly in sample 35 (text-fig. 5) which came from just below the top of Bed 1 at Merstham. In general the species which were shortly to disappear completely had already much declined in this sample, *Tritaxia tricarinata*, *Spiroplectinata* cf. *complanata*, *Dorothia gradata*, *Plectina ruthenica*, *Hagenowella advena*, *Pernerina* sp. and *Gavelinella baltica* (though *Pseudovalvulineria* sp. had a brief maximum). Species which occur in Bed 1 but which are much commoner in Bed 2 have already much increased, e.g. *Textularia chapmani*, *Anomalinoidea globosa*, and *Cibicides* cf. *turonica*. And Bed 2 immigrants were absent or still very scarce, e.g. *Reophax* sp., *Siphogaudryina* sp., and *Gaudryina* sp. The intermediate character of this sample was not due to contamination, for burrows carrying Bed 2 material were carefully removed before preparation. The relative scarcity of Bed 2 immigrants shows that contamination was in fact successfully avoided. Sample 114 at Pitstone from a corresponding stratigraphical position has the same intermediate character.

At this point it is worth recapitulating the main features of the change at the base of Bed 2. They are as follows: the appearance of normal aragonitic fossils, an increase in mud content, certain signs of erosion at the base of Bed 2, and an abrupt change in the non-aragonitic elements of the fauna towards a shallower-water type.

Firstly, as explained above, the appearance of aragonitic forms in the fauna is certainly preservational and probably indicates a decrease in the total CO₂ content of the bottom water which could well be due to a rise in temperature, possibly consequent on a shallowing. It corresponds to the appearance of aragonitic fossils in such shallow-water bands of the Chalk as the Chalk Marl, Chalk Rock, and Top Rock.

Secondly, the increase in mud content at the base of Bed 2 is very temporary and cannot itself be directly responsible for the main features of the faunal change. This is shown by the fact that a much greater increase at the base of Bed 1 was accompanied by a much smaller faunal change and also by the close resemblance between the faunas of Beds 2 and 3 despite the fact that Bed 3 is a chalk. However, as suggested elsewhere

Sample 36, 0-3 ins. above base 2.Sample 35, 0-1½ ins. below 2.Sample 34, 6-10 ins. below 2.

TEXT-FIG. 5. Premonitory changes in the microbenthos at the top of Bed 1 at Merstham. Species which increase or appear at the base of Bed 2 are stippled. Species which become extinct are cross-hatched.

(Jefferies 1961), it is likely that most Chalk marl bands are connected with a fall in erosion base and that this fall was connected with a shallowing of the sea.

Thirdly, the indications of erosion at the base of Bed 2 are not entirely conclusive but it is plausible to connect them with the increase in mud content at the base of Bed 2 and to regard them as due to shallowing.

Fourthly, the reasons for thinking that the change in the fauna at the base of Bed 2 was towards a shallower-water type are as follows:

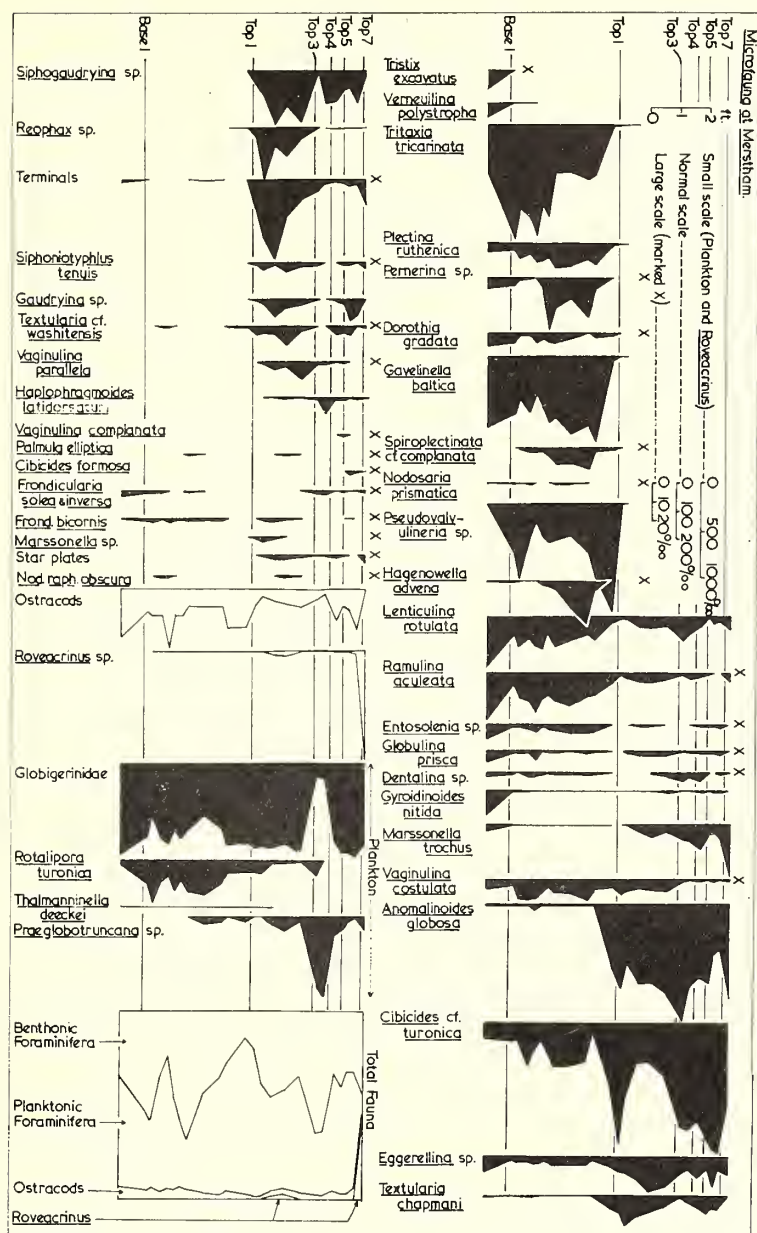
(i) There are a few macrofossils which appear at the base of Bed 2 in the area of standard succession and which had shallow-water distribution or shallow-water relatives in the upper *subglobosus* Zone; these include *Discoidea minima* (cf. *D. subuculus* in the *subglobosus* Zone), *Cidaris lirudo*, *C. perornata*, and bryozoa. However, *Orbirlynchia multicostata*, which had had shallow-water distribution in late *subglobosus* Zone times, died out at this level.

(ii) Examination of the table shows that species of microbenthos with shallow-water distribution or shallow-water relatives in late *subglobosus* times are apt to increase or appear in the area of standard succession at the base of Bed 2 while those with deep-water distribution or relatives in late *subglobosus* times are apt to disappear. There are, however, certain exceptions to this rule; thus *Plectina ruthenica*, *Hagenowella advena*, and *Pseudovalvulineria* sp., which had had shallow-water distribution in late *subglobosus* times, nevertheless died out at the base of Bed 2.

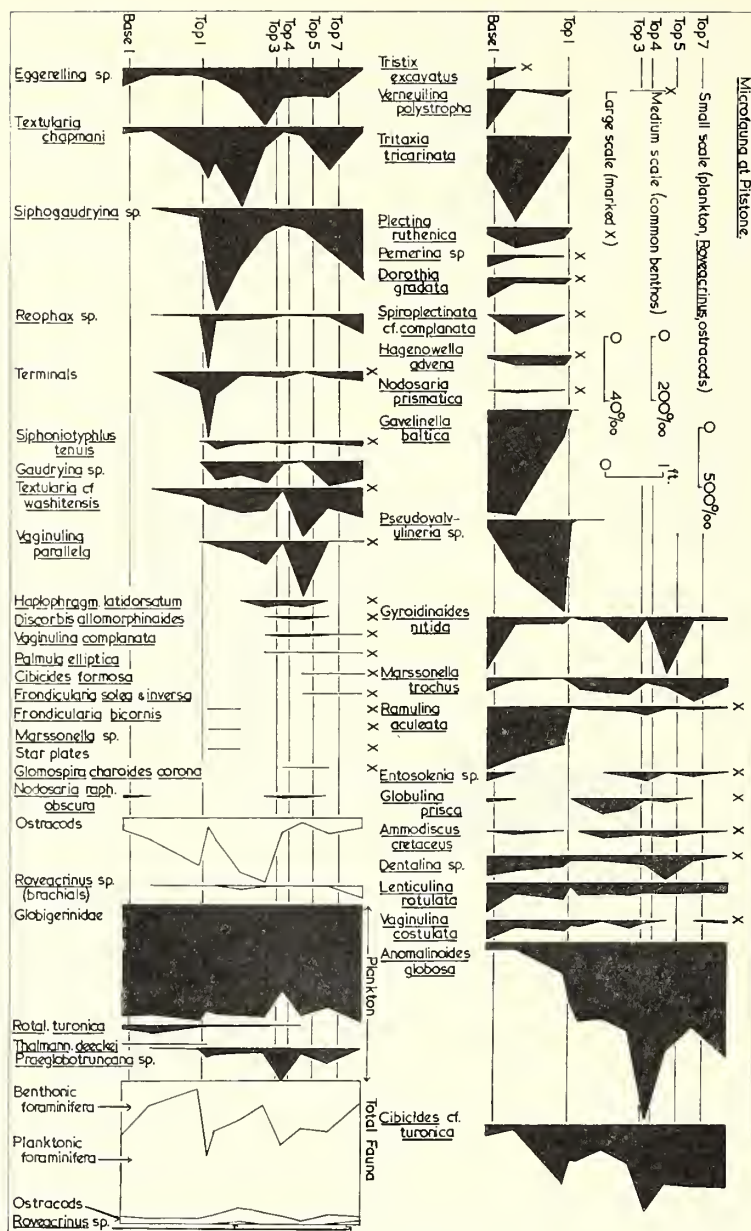
(iii) Some of the forms which appear in Bed 2 in the area of standard succession had relatives in the lower part of the *varians* Zone which was deposited in shallow water, viz. *Siphogaudryina* sp. (cf. *Siphogaudryina* sp. of Burnaby, fig. 1), *Quinqueloculina antiqua* (cf. *Quinqueloculina* sp. of Burnaby, loc. cit.), '*Rhynchionella*' *lineolata carteri* (also found in the Cambridge Greensand), and *Plicatula barroisi* (cf. *P. sigillina* of the Cambridge Greensand).

(iv) Some of the forms which increase at the base of Bed 2 have shallow-water relatives in Recent seas. Thus *Quinqueloculina* (represented by *Q. antiqua* in Bed 2 at Eastbourne and Crésantignes) is at present commonest at a depth of 30–40 metres (Curtis 1955, p. 268) and is usually regarded as characteristic of shallow water (Lowman 1949, Phleger and Parker 1951). Similarly *Cibicides* cf. *tuironica* becomes much commoner at the base of Bed 2 and *Cibicides* in the Gulf of Mexico is commonest above a depth of 220 metres. Bryozoa and asteroidea (*Crateraster quinqueloba* and *Calliderma smithiae*), which respectively enter and become much commoner at the base of Bed 2, are also mainly of shallow-water distribution at the present day.

Shallow water is usually more turbulent and also warmer than deep water. From the point of view of lithology, in particular the deposition of mud and cutting of erosion surfaces, turbulence is more important than temperature. For ecology and the preservation of aragonite, however, temperature is more important than turbulence. Hutchins (1947) has emphasized the importance of temperature to modern marine animals and it has often been invoked to explain the distribution, and in particular the depth zonation, of benthonic foraminifera. For instance, Norton (1930, p. 332) in the West Indies and Natland (1933, p. 227) off California, defined their foraminiferal depth zones in both fathoms and degrees centigrade. Parker (1948, p. 231) used temperature and annual temperature range to explain the depth zonation of benthonic foraminifera south of Cape Cod and also the differences in the faunas north and south of the Cape. Phleger



TEXT-FIG. 6. The microfauna at Merstham.



TEXT-FIG. 7. The microfauna at Pitstone.

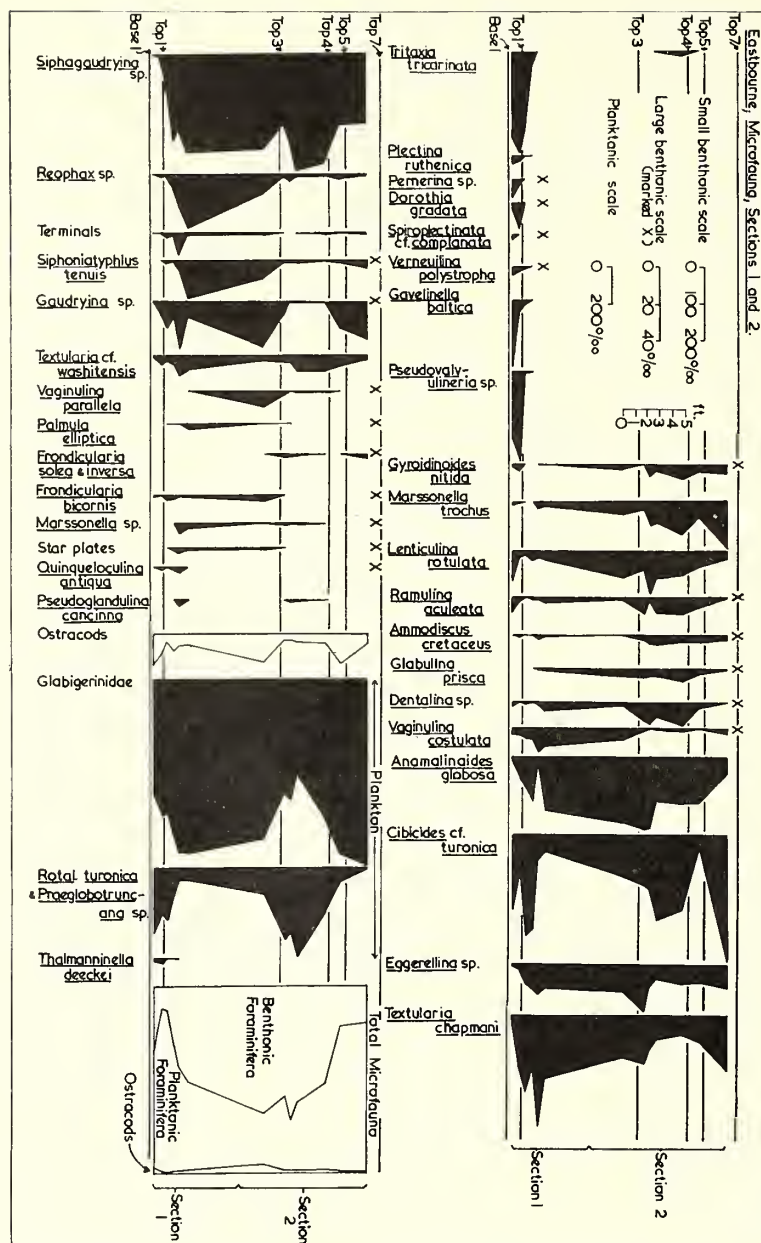
(Phleger and Parker 1951, pt. 1, p. 50) remarked that the top of the main thermocline in the Gulf of Mexico, at about 100 metres, coincided with a very great faunal change. He noted, however, that penetration of light, agitation of the bottom, and great annual temperature range also distinguished the depths above 100 metres from the depths below. Crouch (1952), when studying the distribution of foraminifera in submarine basins off the coast of California, concluded that the foraminiferal fauna at the bottom of a basin correlated better with sill-depth (i.e. temperature) than with true depth. And Resig (1958, p. 302) confirmed a change in the benthonic foraminifera at sill-depth in the Santa Cruz basin in the same general area. Bandy (1953), also working off California, agreed that temperature was an important factor, though not the only one, and he has also confirmed (1956, p. 189) Phleger's conclusion that temperature was important in the Gulf of Mexico. This does not mean that the pattern of distribution of foraminifera always depends on temperature as has been neatly demonstrated by Said (1950) in the strange hydrographical conditions of the Red Sea. In this sea something resembling the normal depth zonation is present (*Quinqueloculina* common in shallow water, *Uvigerina* at depth) but this cannot be due to temperature which has a total range of less than 2° C., with the lowest temperatures at middle depths, not at the bottom. Similarly Resig (1958) found zonation even in the isothermal parts of the Santa Cruz Basin. The results of these workers, however, do not show that temperature is unimportant in the cases where it has been invoked, but only that under rather unusual conditions it is not the main cause of faunal variation in benthonic foraminifera.

It is therefore likely that the change at the base of Bed 1, though it caused greatly increased turbulence resulting in erosion and muddiness, nevertheless caused little rise in temperature and therefore had little effect on the fauna or on the preservation of aragonitic fossils. The change at the base of Bed 2, on the other hand, caused little increase in turbulence but a strong rise in temperature of the bottom water which led to the preservation of aragonitic fossils and an abrupt change in the other elements of the fauna. The supposition that the change at the base of Bed 2 was largely due to a rise in temperature explains why it seems to have occurred at Bellignies (text-fig. 11) where the water was so turbulent throughout *plenus* times that the succession was condensed.

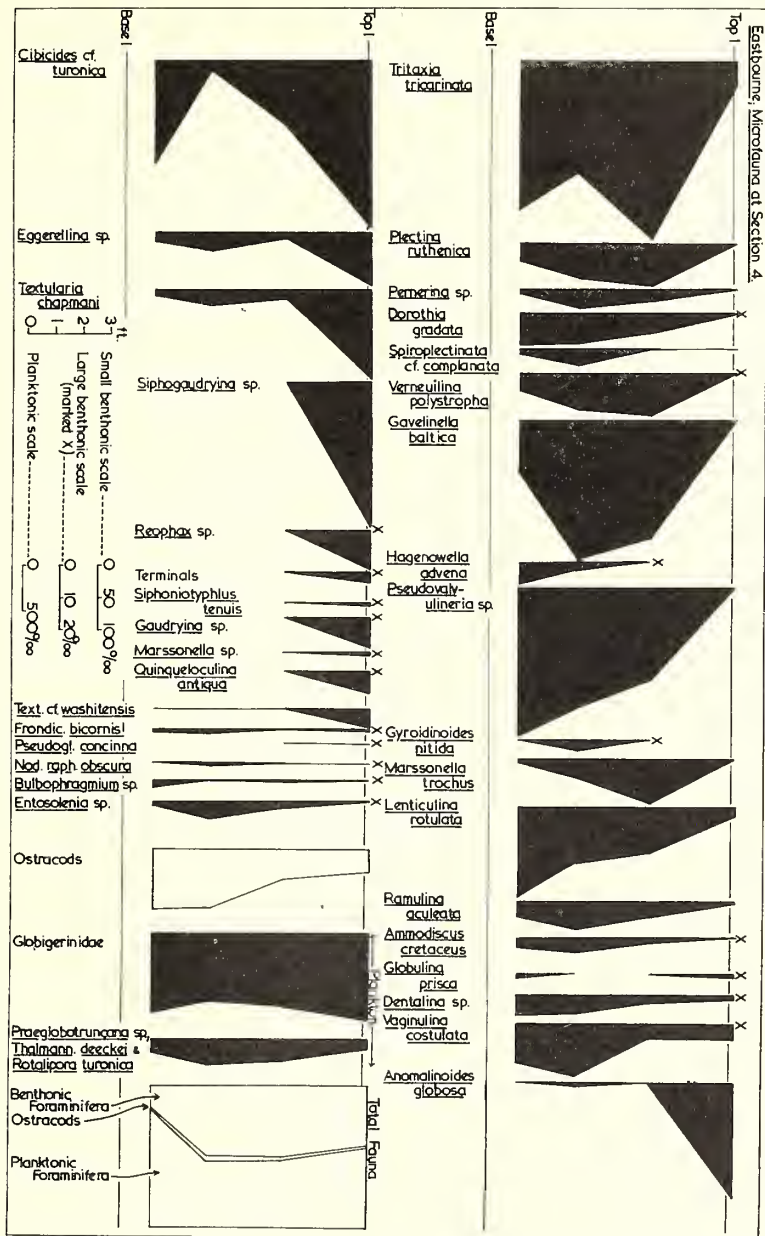
The change in temperature at the beginning of Bed 2 times was probably greater than the difference in temperature between Pitstone and Cap d'Antifer in late *subglobosus* times or the increase in temperature at the beginning of Bed 1 times. This would explain why some species with a shallow-water distribution in the top of the *subglobosus* Zone and which increase in the area of standard succession at the base of Bed 1 (viz. *Plectina ruthenica*, *Hagenowella advena*, *Pseudovalvulineria* sp., and *Orbirhynchia multicostata*) nevertheless disappear at the base of Bed 2.

The disappearance of *Lingula* sp. at the top of Bed 1 is also anomalous for this species belonged to a genus well known for its shallow-water habits in Recent sea. However, this particular species is present throughout the Lower Chalk up to this level, being especially common at the top of the *subglobosus* Zone, and shows no sign of shallow-water preferences. Its disappearance at the base of Bed 2, along with most other species common in Bed 1 and the *subglobosus* Zone, is therefore not surprising.

The actual values of bottom-water temperature for Bed 1 and the *subglobosus* Zone cannot be estimated with certainty. However, Bed 1, *ex hypothesi*, was laid down in water colder than the equilibrium temperature of aragonite which under modern



TEXT-FIG. 8. Eastbourne, microfauna, sections 1 and 2; exact localities given in Jefferies (1961).



conditions, at least in the laboratory, is 5–10° C. (see above). Bed 2 was laid down in water warmer than this equilibrium temperature, and, as will be argued below from the nature of the fauna, in water somewhat warmer than Beds 4–6. The latter, on the basis of O¹⁸ analyses of *Actinocamax plenus* which must almost certainly have come from them, may have been laid down at a temperature of about 16.9° C. (Lowenstam and Epstein 1954).

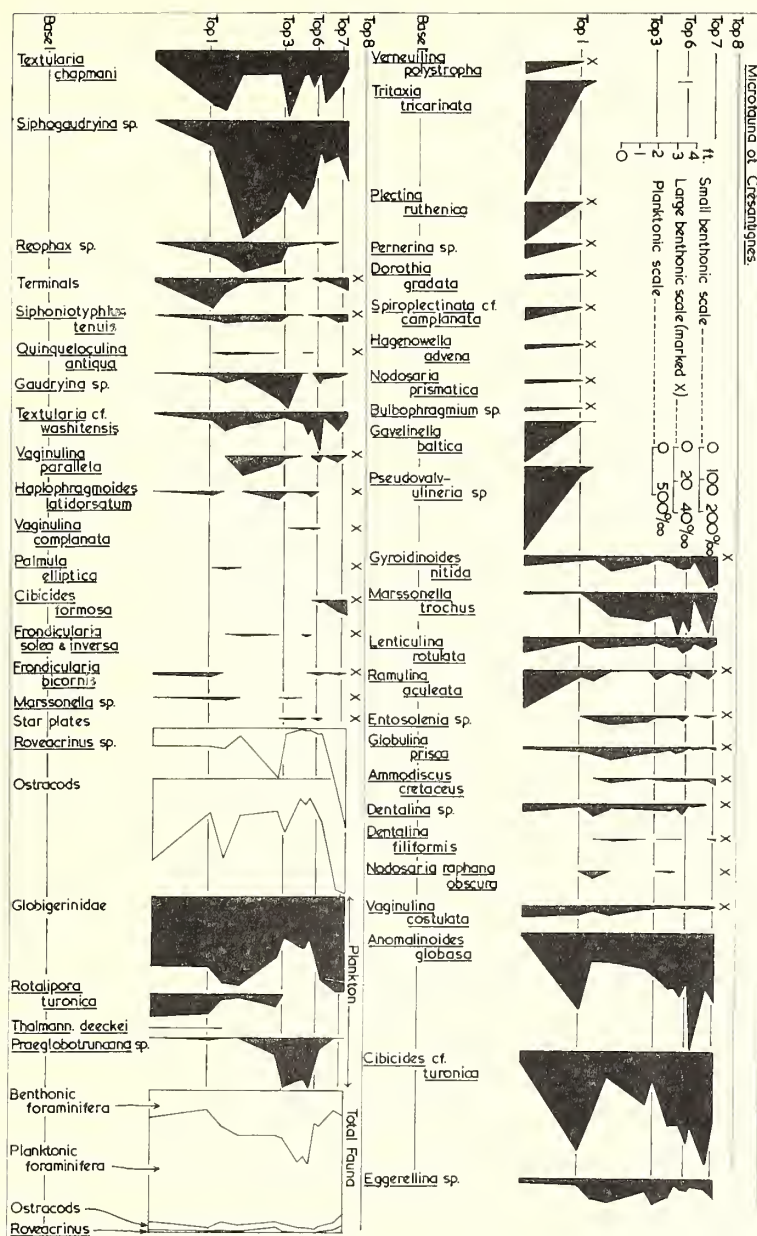
Finally it is interesting to note certain analogies between the change at the base of Bed 2 and the change at the top of the Ma division of the Dutch Maestrichtian. In Ma, Visser (1951) has recorded a fauna with abundant *Plectina ruthenica* and *Pseudovalvulineria lorneiana*. This gives place to a fauna in the stratigraphically higher Mb and Mc divisions which, in one locality, contains abundant *Quinqueloculina* and *Heterostomella*. The Ma fauna recalls Bed 1 (with *Plectina ruthenica* and *Pseudovalvulineria* sp.) whereas the Mb and Mc fauna recalls Bed 2 (with *Quinqueloculina antiqua* and *Siphogaudryina* sp. which resembles *Heterostomella*). This change in the Dutch Maestrichtian is usually taken to be a shallowing or a rise in temperature (which led to the invasion of Tethyan forms, including rudists).

The occurrence of *Ornatolthyris* sp. in Bed 2 or the base of Bed 3 from Marham roughly as far south as Tring coincides with the area in which Bed 2 is very thin or absent and in which, therefore, the sub-Bed 2 erosion surface was for a long time exposed on the sea bed. This probably favoured *Ornatolthyris* sp. by providing a suitable surface for pedicle attachment. The northern distribution of this species is connected with the fact that all through the Cenomanian the genus was almost confined to Yorkshire and Lincolnshire.

Beds 2–3 and 3. Most macrofossils are rarer in Beds 2–3 and 3 than in Bed 2 though they are easier to collect because Bed 2 is often very thin. The fossils which so decline include all the commoner calcitic species (except *Inoceramus pictus*) such as the large gryphteate form of *Ostrea vesicularis* (which seems never to occur higher than the top of Bed 2), '*Rhynchonella*' *lineolata carteri*, *Terebratulina striatula*, *T.* cf. *nodulosa*, *Entolium membranaceum*, *Calliderma smithiae*, and *Crateraster quinqueloba*. The aragonitic species *Grammatodon* cf. *cenomanense*, *Cerithium* sp., and *Protocardia hillana* also seem to decline. On the other hand, *Metoicoceras geslinianum* does not decline so quickly as most other species, and *Solarium* sp. and *Aporrhais* sp. are commoner in Bed 3 than in Bed 2. The result is an increase in the ratio of aragonitic to calcitic forms but a decline in the absolute numbers of both groups. One other important change in the macrofauna is the appearance of *Actinocamax plenus* as a rarity at the top of Bed 3. This represents the start of the North Boreal invasion which is much more important in Bed 4. These changes coincide with a decline in mud content and probably, therefore, if the theory of origin of marl bands postulated in Jefferies (1961) is correct, with an increase in the rate of deposition. Most of the calcitic fossils which decline from Bed 2 to Bed 3 increase again in Bed 4 (which marks an increase in mud content and possibly a decrease in the rate of deposition). It therefore seems likely that the abundance (per unit volume of rock) of these species was controlled either by a liking for mud, or else tended to be merely inversely proportional to the rate of deposition.

In the microfauna there are local inconsistencies but the main changes are as follows:

(i) *Anomalinoidea globosa* and *Cibicides* cf. *turonica* reach a peak in, or occasionally



TEXT-FIG. 10. Microfauna at Crésantignes.

just below, Bed 2 (Crésantignes, Eastbourne, Pitstone, and Merstham), tend to decline in Bed 2–3, and then often increase again up to the top of Bed 3 (Pitstone, Eastbourne, Merstham, but not Crésantignes).

(ii) *Reophax* sp., *Textularia chapmani*, *Siphogaudryina* sp., and *Siphoniotyphlus tenuis* commonly increase to a peak in Beds 2–3 (at a somewhat higher level than *A. globosa* and *C. cf. turonica*) and then decline again towards the top of Bed 3. Exceptions to this generalization are at Pitstone (text-fig. 7) where *Reophax* sp. reaches a peak in Bed 2 instead of in Beds 2–3 and at Eastbourne (text-fig. 7) where *Siphogaudryina* sp. does not show a definite peak in Beds 2, 2–3, or 3.

(iii) *Quinqueloculina antiqua* and *Marssonella* sp. die out at the top of Bed 2.

(iv) The group of temporary absentees or rarities in Bed 2 increase above that Bed, i.e. *Lenticulina rotulata*, *Dentalina* sp., *Ammodiscus cretaceus*, *Marssonella trochus*.

These changes can be interpreted in terms of change in temperature and mud content. Temperature probably increased to a maximum during the deposition of Beds 2–3 and then decreased again. This is suggested by the fact that three Bed 2 immigrants, which should be thermophile, have a maximum at about that level, viz. *Siphoniotyphlus tenuis*, *Siphogaudryina* sp., and *Reophax* sp. The decline in temperature at the top of Bed 3 is confirmed by the occasional presence at that level of the 'North Boreal' *Actinocamax plenus*. The effect of fall in mud content can probably be seen in the disappearance of *Quinqueloculina antiqua* which was probably a mud-lover as shown by its abundance at Bellignies.

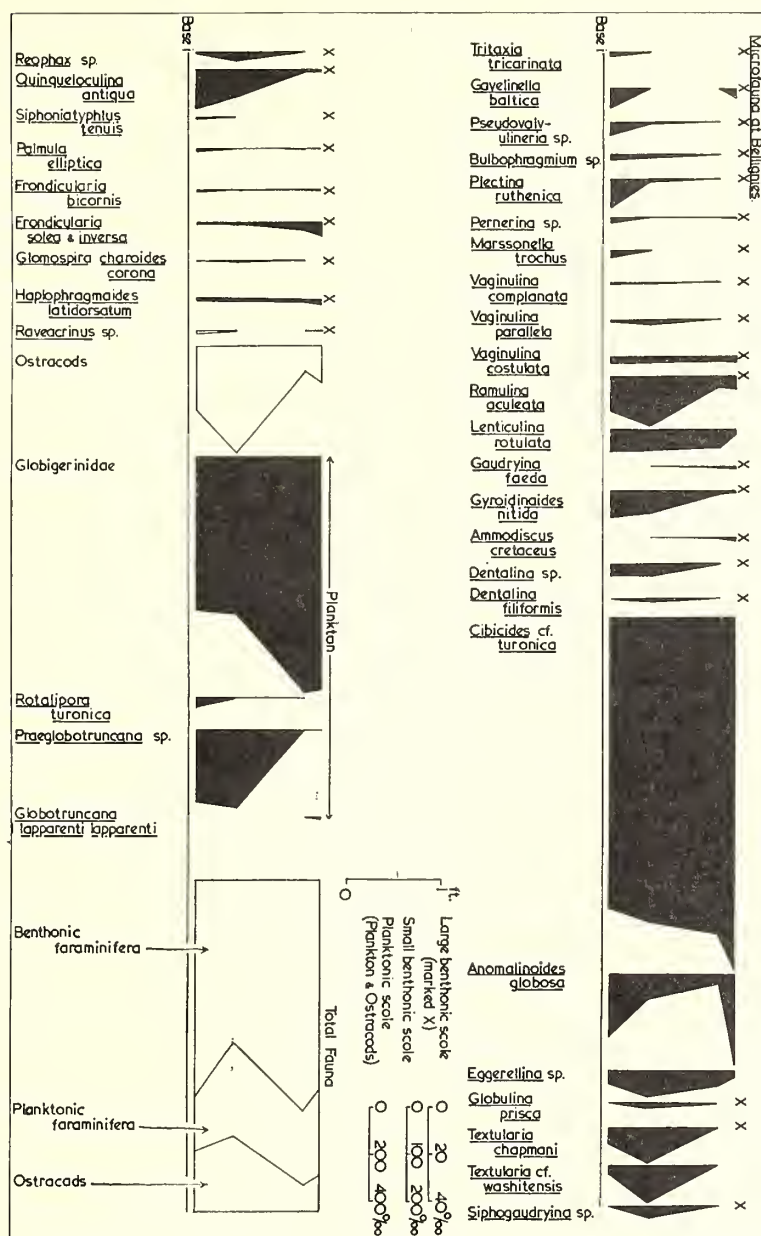
Beds 4, 5, and 6. The macrofauna of Beds 4, 5, and 6 is very like that of Beds 2 and 3 but there are certain differences which suggest a lower temperature of deposition. It can be divided into the following distributional groups:

(i) '*Rhynchonella*' *lineolata carteri*, *Entolium membranaceum*, *Crateraster quinqueloba*, *Terebratulina striatula*, *T. cf. nodulosa* are significantly commoner in Beds 4 and 6 than in Beds 5 or 3 (and had also tended to be commoner in Bed 2 than in Bed 3). It seems likely that the abundance of this group was controlled either by muddiness or by rate of deposition, or by both.

(ii) Some macrofossils are found almost exclusively in Beds 4–6, viz. *Oxytoma seminudum* (also found rarely in Bed 2, however), *Ditrupa difformis* (mainly in the South Downs), *Actinocamax plenus* (also rarely in the top of Bed 3), and *Aequipecten arlesiensis*. *Plicatula barroisi* is much commoner in Bed 4 than above or below. The abundance of *Actinocamax plenus* in these beds is particularly striking, for belemnites of any sort are very rare in the English Chalk for hundreds of feet above and below.

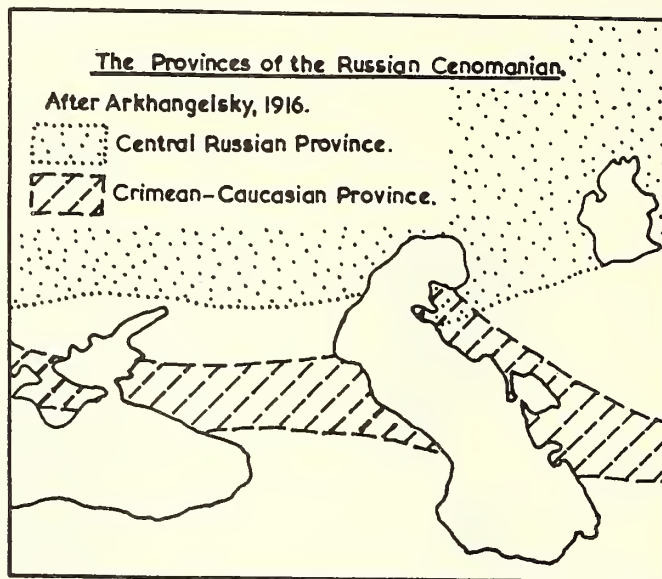
(iii) Aragonitic fossils are common in Beds 4–6 only where the Subzone is more than about 10 feet thick (possibly in connexion with decreased temperature and increased turbulence) and the ammonites belong to the *gourdoni*, not to the *gelsinianum* fauna.

In trying to explain the faunal peculiarities of Beds 4–6 the work of Arkhangel'sky (1916) is important. This author recognized two main types of Cenomanian in European Russia (text-fig. 12). In the north and as far south as the southern Ukraine occurred the 'Central Russian' (or more strictly the Central European Russian) Type. This was characterized by the abundance of forms which Arkhangel'sky identified as *Actinocamax primus* Arkhangel'sky, *Pteria pectinata* (Sowerby), *Pecten robinaldinus* d'Orbigny, and



Exogyra conica (Lamarck). Ammonites, particularly *Acanthoceras*, were rare, but species of *Schloenbachia* occurred. South of this area was the Crimean-Caucasian Type in which *A. primus*, *P. pectinata*, *Pecten robinaldinus*, and *E. conica* were rare or absent, but in which ammonites were commoner and included *Acanthoceras*, *Turrilites*, and *Scaphites* as well as *Schloenbachia*. The difference between the two areas was largely one of temperature (Arkhangelsky 1916, p. 95).

The interest of Arkhangelsky's work, from the present point of view, is that two, and possibly three, of the index species of the 'Central Russian' Province had close relatives



TEXT-FIG. 12. The provinces of the Russian Cenomanian.

among the forms characteristic of Beds 4–6. Thus *Actinocamax primus* was very similar to *A. plenus* and possibly a direct ancestor (Jeletzky 1948). *Pteria* (*Oxytoma*) *pectinata* (Sowerby), as described by Woods (1905, p. 59), is very like *Oxytoma seminudum* (Dames) and the form mentioned by Arkhangelsky may really have been *O. seminudum* for the type of the latter came from the Cenomanian of north Germany, whereas the type of *P. pectinata* came from the Lower Albian Folkestone Sands. Also Arkhangelsky's *Pecten robinaldinus* d'Orbigny may possibly be related to *Aequiptecten arlesiensis* for both species have the same type of imbricate ribbing (Woods 1902, p. 181). It therefore seems reasonable to suppose that the occurrence, certainly of *Actinocamax plenus* and *Oxytoma seminudum*, and possibly of *Aequiptecten arlesiensis*, in Beds 4–6, indicates a fall in temperature by analogy with the distribution of their close relatives in the Russian Cenomanian.

There is other evidence besides Arkhangelsky's that *Oxytoma seminudum* and *Actinocamax plenus* had northern affinities. Thus *O. seminudum*, even in the Cenomanian of western Europe, is commoner in the north than the south; it is, firstly, one of the characteristic fossils of the *subglobosus* Zone of Yorkshire (= *varians* Zone of southern England) (Wright and Wright 1942, p. 115) but is certainly rare in the *varians* Zone of

southern England; secondly it is often abundant in the Cenomanian pebbles of north Germany (Noetling 1885, table p. 48); and thirdly it is common in the Cenomanian of Northern Ireland (J. M. Hancock, personal communication). In addition to this *Oxytoma semimudum* is very nearly identical to *O. tenuicostatum* (Römer) (Cox 1939, p. 18) and *O. tenuicostatum*, according to Naidin (1959, p. 129), is a 'typical boreal form' in the Upper Cretaceous of the Russian platform. With regard to *Actinocamax plenus* it is worth noting that Jeletzky (1950, p. 22) has postulated that *Actinocamax* in the Turonian Favel Formation of Manitoba had spread into that area from permanently cold, more northerly waters. Also the genus *Actinocamax* is regarded by Naidin (1959, p. 129) as characterizing the north-eastern and colder parts of the Russian Platform in the Upper Cretaceous whereas the warmer, south-western parts had either almost no belemnites, or else, in the Senonian, had mainly *Gonioteuthis*. A particular case of this is the distribution of *Actinocamax intermedius* Arkhangelsky which is a characteristic fossil of the Upper Turonian in the north-eastern part of the Russian Platform (Naidin 1960, p. 47) at which horizon belemnites are virtually unknown in England or northern France.

The resemblance of the index species of Beds 4–6 to the index species of Arkhangelsky's 'Central Russian' area does not prove that the population of these species in Beds 4–6 of the Anglo-Paris Basin had actually descended from immediate Central European Russian ancestors. In fact, even if this were true, it could never be demonstrated. This is because the Upper Cenomanian, except in the Lvov-Lublin Basin, is everywhere missing in the 'Central Russian' area (Naidin 1960, p. 45) and Upper Turonian rests directly on Lower Cenomanian. Besides this the Cenomanian belemnite of the 'Central Russian' area is *A. primus* and only farther south and west, in extra-Russian Europe, Moldavia and the Ukraine does *A. plenus* occur (Naidin 1954, fig. 2, p. 20). Naidin has suggested (*loc. cit.*) that this was a case of contemporaneous geographical subspeciation with *A. primus* adapted to colder and *A. plenus* to warmer water. If this were true the *A. plenus* in Beds 4–6 in the Anglo-Paris Basin could clearly not have had immediate ancestors in the 'Central Russian' area where only *A. primus* occurred. However, Naidin's interpretation is probably over-simplified since, according to Jeletzky (1948, p. 341), far from being contemporaneous, *A. primus* characterizes Lower and *A. plenus* Upper Cenomanian. The mutually exclusive areas of distribution of the two species shown in Naidin's map (1954, fig. 2) seem to reflect the interaction of four facts, viz. the commonness of *A. primus* in the Lower Cenomanian of Arkhangelsky's 'Central Russian' area; the absence of Upper Cenomanian and Lower Turonian from that area; the presence in extra-Russian Europe of Lower Turonian deposits with abundant *A. plenus*; and the very great rarity of all *Actinocamax* in the Cenomanian of extra-Russian Europe. In view of this the *A. plenus* in Beds 4–6 of the Anglo-Paris Basin could well have had immediate Central European Russian ancestors all trace of which has been lost because of the non-preservation of Upper Cenomanian rocks in that area. However this may be, the important point is that *Actinocamax plenus* and *Oxytoma semimudum* (almost certainly) and *Aequipecten arlesiensis* (quite possibly) spread into the Anglo-Paris Basin during the deposition of Beds 4–6 from somewhere where the water was cooler. Whether they came from Central European Russia or Greenland (from which Swinnerton (1943) has recorded a probably Senonian fauna of *Actinocamax*) or any other northern area is much less important.

None of the North Boreal index species were found above Bed 6 except for a juvenile *Actinocamax* at the base of Bed 7 at Cr santignes (where the correlation of these few inches of succession is not entirely satisfactory) and another *A. plenus* possibly from Bed 8 at Merstham. This suggests that the cool period which allowed these species to spread into the Anglo-Paris Basin during the time of deposition of Beds 4–6 was followed by an increase in temperature at the beginning of Bed 7 times.

The serpulid *Ditrupa difformis* is in some respects puzzling in its distribution in Beds 4–6. Outside the area of standard succession it seems to have preferred shallow water; it is abundant, for instance, just above the sub-*plenus* erosion surface at Bellignies, in Bed C in Devon, just above the sub-*labiatus* surface near le Mans, and in the shallow-water Cenomanian of Northern Ireland and Cap d'Antifer. Further, Avnimelech (1941) noted that the related *Hamulus octocostatus* was restricted to shallow water in the Campanian of Israel. In view of this liking for shallow water it is surprising that in Bed 4 the species is commonest where the Bed is thick (mainly in Sussex) and the water was presumably deep. This may possibly mean that some of the larvae produced by the prosperous populations round the Ardennes Massif, of which the population at Bellignies was part, settled on the sea bottom in deep water in nearby Sussex but were unable, or not easily able, to reproduce there.

The abundance of *Plicatula barroisi* in Bed 4 is perhaps related to the abundance of *Actinocamax plenus*. The guards of the latter seem to have provided particularly suitable attachment surfaces for the spat for they are often covered with *P. barroisi* which is seldom fixed to anything else.

The benthonic microfauna of Beds 4–6 shows much variation and cannot be interpreted except by comparison with the beds above and beneath. Because of this it will be discussed place by place without confining the discussion to Beds 4–6 alone. At Pitstone (text-fig. 7), which was the northernmost section where the microfauna was studied statistically, the behaviour of *Textularia chapmani*, *Siphogaudryina* sp., *Reophax* sp., asteroid terminals, *Siphoniotyphlus tenuis*, and *Gaudryina* sp. is significant. All these species show a minimum in Beds 4–6 with maxima above and beneath. This is interesting because all except *T. chapmani* and asteroid terminals were Bed 2 immigrants into the area of standard succession, and even the two exceptions greatly increased at the base of Bed 2. This suggests, if the change at the base of Bed 2 was due to a rise in temperature, that all these species were thermophile. Their minima in Beds 4–6 would, therefore, suggest that the water when these beds were deposited was colder than when higher and lower beds were being deposited and this agrees with the occurrence of North Boreal species in the macrofauna. The behaviour of *Cibicides* cf. *turonica* and *Anomalinoidea globosa* in Beds 4–6 at Pitstone is roughly converse to the species just mentioned in that they have maxima in Bed 4 and minima above and beneath. This suggests that Bed 4 was deposited at roughly their optimum temperature, in agreement with their occurrence in Bed 1 (where, however, *A. globosa* is rare) and with the fact that in Beds 2–3 and 3 they usually reach a maximum slightly earlier than the Bed 2 immigrants. The occurrence of *Verneuillina polystropha* in Bed 4 at Pitstone might be thought to confirm the cooling at that level for the species otherwise dies out at the top of Bed 1. The record, however, is based on one specimen and may well be due to sieve contamination. The presence of *Discorbis allomorphinoides* in Beds 4 and 5 at Pitstone is interesting since this species is the commonest benthonic foraminiferan in the 'marnes

à ostracées' of the south-west Paris Basin (area of le Mans) and was not found elsewhere in the area of standard succession. The reasons for its presence at Pitstone are unknown.

At Merstham (text-fig. 6) the benthonic microfauna behaves much as at Pitstone. *Cibicides* cf. *turonica* and *Anomalinoides globosa* reach a maximum in Bed 4 and *Textularia chapmani*, asteroid terminals, *Gaudryina* sp., and *Siphoniotyphlus tenuis*, as at Pitstone, are rarer in Beds 4–6 than above or beneath. However, the counting did not extend high enough to show whether *Reophax* sp. becomes common again at the base of the Melbourn Rock as at Pitstone. There are also some differences from Pitstone. Thus *Siphogaudryina* sp. at Merstham, though it has a minimum at the base of Bed 4, has a maximum at the top of that bed; *Textularia* cf. *washitensis* is definitely rarer in Beds 4–6 than above or beneath, agreeing with the fact that it greatly increases at the base of Bed 2, but differing from the situation at Pitstone; *Gyroidinoides nitida* is definitely rarer in Beds 3 and 4–6 than at Pitstone; and *Discorbis allomorphinoides* was not found at Merstham. Some of these differences between the two sections may represent a southward decline in the cold-water current of Beds 4–6 (though the behaviour of *T.* cf. *washitensis* is anomalous). One must also take into account, however, the fact that the extraction at Merstham was on average only half as successful as at Pitstone.

At Eastbourne (text-fig. 8) the behaviour of the benthonic microfauna in Beds 4–6 is rather different from Merstham or Pitstone. The most striking fact is the occurrence of *Tritaxia tricarinata* at the top of Bed 4 (23 specimens counted). This species had temporarily disappeared at the beginning of Bed 2 times in the area of standard succession and was consequently probably thermophobe. Its reappearance would therefore suggest cooling. Why the species did not reappear at the two more northern localities is not clear but the ecological control of a rare species may be even more subtle than that of a common one. At both Eastbourne and Crésantignes there are maxima in *Textularia chapmani*, *Eggerellina* sp., and *Gaudryina* sp. immediately above the base of Bed 4. These maxima do not occur at Merstham or Pitstone where Bed 4 is thinner and this suggests that at the two more northern localities the lowest parts of Bed 4 have wedged out against the sub-Bed 4 erosion surface. Excluding these short-lived maxima, however, the thermophile species *Gaudryina* sp., *Siphoniotyphlus tenuis*, perhaps *Textularia chapmani*, and asteroid terminals are generally rarer at Eastbourne in Beds 4–6 than above or beneath. On the other hand, *Siphogaudryina* sp. has a definite maximum in Bed 4 and in this respect the signs of cooling in Beds 4–6 at Eastbourne are less clear than at Pitstone. Counting did not extend high enough at Eastbourne to show whether *Reophax* sp. becomes common again at the base of the Melbourn Rock.

At Crésantignes the thermophobe *Tritaxia tricarinata* also recurs, probably in Bed 5. The thermophile *Siphoniotyphlus tenuis* and asteroid terminals, and also, in a general way, *Gaudryina* sp. are rarer in Beds 4–6 than above or beneath (except for the maximum of *Gaudryina* sp. at the base of Bed 4) and, again, counting did not extend high enough to show whether *Reophax* sp. increases again at the base of the Melbourn Rock. *Siphogaudryina* sp. behaves much as at Eastbourne.

Thus the benthonic microfauna of Beds 4–6 shows signs of the cooling deduced from the macrofauna in two ways: (i) The rarity of thermophile species, most of which had immigrated into the area of standard succession at the beginning of Bed 2 times, as compared with the beds above and beneath. This phenomenon is clearer at Pitstone

than at Merstham and clearer at Merstham than at Eastbourne or Crésantignes; it thus seems to weaken southwards. (ii) At Eastbourne and Crésantignes, but not in the two more northern sections, *Tritaxia tricarinata* recurs in the top of Bed 4 or Bed 5.

The southward weakening in the oscillation in thermophile species suggests an influence spreading from the north and this agrees with conclusions derived from the macrofauna. On the other hand, the southern distribution of the recurrence of *Tritaxia tricarinata* points in the opposite direction, but this is a phenomenon on a very much smaller scale.

Among the planktonic foraminifera the most striking features of the distribution in Beds 4–6 are as follows: (i) *Rotalipora turonica* dies out in Bed 4. (ii) *Praeglobotruncana* sp. has a maximum in Bed 4. (iii) Globigerinidae have a minimum in Bed 4 which is almost exactly converse to the maximum in *Praeglobotruncana* sp.

Because there are so few species involved, and because none of them are parallel in behaviour to any benthonic species, it is not possible to interpret these changes ecologically with any confidence. It seems possible, however, that the extinction of *Rotalipora turonica* may have been due to the maximum of *Praeglobotruncana* sp., for the two species are rather similar and may therefore have been competitors.

The fauna of Beds 4–6 is more like that of Beds 2 and 3 than like that of Bed 1. In particular only one of the species (*Tritaxia tricarinata*) which disappeared as a result of the warming at the beginning of Bed 2 times attempted to return during the deposition of Beds 4–6 and even it was much less common than in Bed 1. These facts suggest that, although Beds 4–6 were deposited in colder water than Beds 2 and 3, Bed 1 was deposited in much colder water still. In view of this, however, it is difficult to explain why the index species of the cooling during the deposition of Beds 4–6 (*Actinocamax plenus*, *Oxytoma seminudum*, and *Aequipecten arlesiensis*) had not already appeared in the area of standard succession during the deposition of Bed 1. Evidently if the temperature of deposition of Bed 1 was suitable for these species (which may, however, have been stenothermal rather than thermophobe) then some other factor must have been unsuitable. Further work would be needed to discover what it was.

Beds 7 and 8. The macrofauna of these beds is very like that below except that: (i) The North Boreal index species have died out. (ii) *Orbirhynchia wiesti* is common in Bed 7 and rare above or beneath. The microfauna has already been dealt with under Beds 4–6.

The ecology of the condensed succession at Bellignies. The vertical distribution of the fauna at Bellignies (text-fig. 11) is interesting because it suggests that the faunal change which occurred at the beginning of Bed 2 times in the area of standard succession also occurred at a locality where the succession was condensed. It also seems to show the ecological effect of high mud content for the matrix is a plastic green clay.

With regard to the first point the actual age of the 'tourtia de Mons' (Bed i) at Bellignies, as judged by the macrofauna (Jefferies 1961), is probably the same as Beds 4–6 of the standard succession and the greater part of the benthonic microfauna is certainly younger than Bed 1. Especially in the lowest sample shown in text-fig. 11, however, a number of species occur which must be of Bed 1 age or earlier, viz. *Tritaxia tricarinata*, *Gavelinella baltica*, *Pseudovalvulineria* sp., *Plectina ruthenica*, *Pernerina* sp. The preservation of these species is no different from the rest of the microfauna, suggesting that they

are not earlier than Bed 1 or late *subglobosus* Zone in age. Even if they are derived from the Middle Cenomanian 'sarrasin' beneath the 'tourtia', it is evident that a change analogous to the change at the beginning of Bed 2 times also occurred at Bellignies, although it may have happened much earlier. An attempt to extract a microfauna from the hard sugary 'sarrasin' was unsuccessful.

The effect of the muddiness of the matrix can probably be seen in the extreme abundance of *Entolium membranaceum* in the macrofauna for, as explained above, the distribution of this species in the standard succession suggests a liking for mud. Also, in the microfauna, the effect of muddiness may perhaps be seen in the large size of *Quinqueloculina antiqua* (agreeing with its disappearance at the top of Bed 2), the rarity of *Marssonella trochus* (agreeing with its decrease at the base of Bed 1), the absence of *Gaudryina* sp. and the absence of bryozoa, which, as a phylum, prefer clear water (Buge, in Piveteau 1952, p. 738).

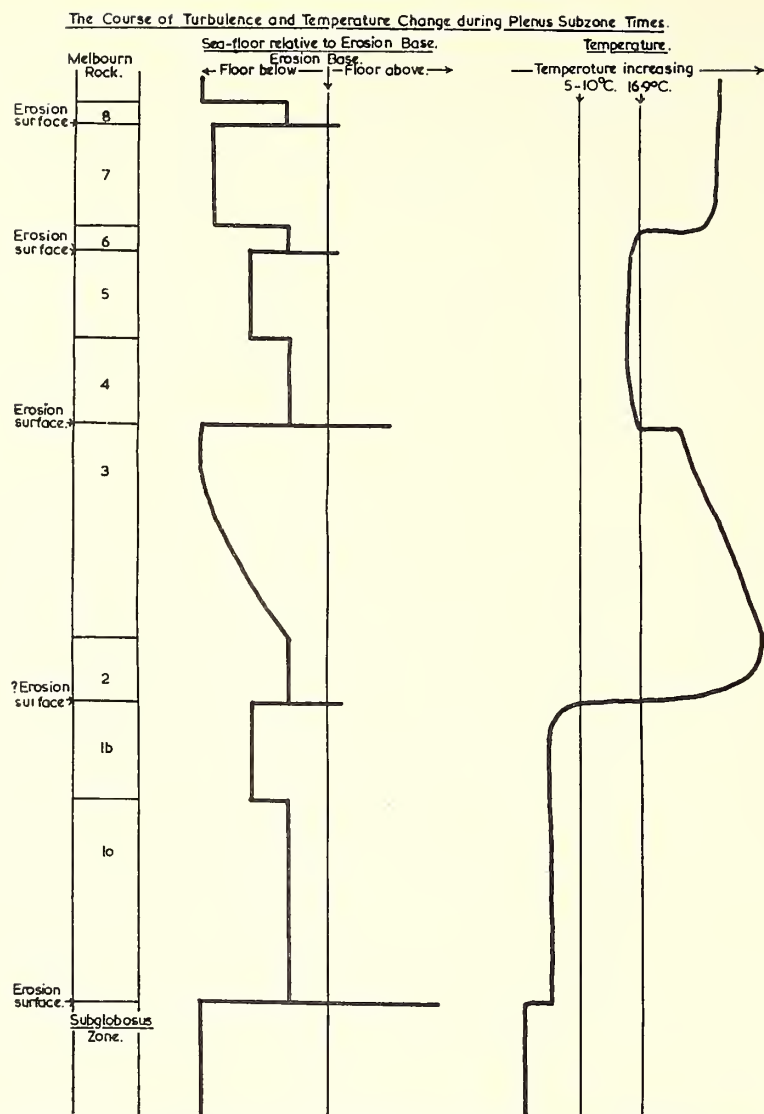
CONCLUSIONS

In a general way it is therefore possible to reconstruct temperature changes from the end of *subglobosus* times to the time of deposition of the base of the Melbourn Rock. The temperature of Bed 1 times was higher than that of *subglobosus* Zone times but not much higher or there would have been more faunal change. Both Bed 1 and the upper *subglobosus* Zone were laid down below the equilibrium temperature of aragonite which may have been about 5–10° C. The temperature of deposition of Bed 2 was very much higher than that of Bed 1 and higher than the equilibrium temperature of aragonite or the temperature of deposition of Beds 4–6 and the increase in temperature at the beginning of Bed 2 times took place during the deposition of only a few inches of rock. It is likely, however, that deposition was rather slow at this time. Temperature rose to a maximum at the start of deposition of Bed 3 and then declined again. Eventually it fell so low that 'North Boreal' macrofaunal species of central European Russian affinities spread into the Anglo-Paris Basin during the deposition of Beds 4–6. The temperature of deposition of these beds, however, as judged by the nature of the fauna, was still higher than that of Bed 1, and, on the evidence of O¹⁸ analysis of belemnites probably from this level, it may have been about 16.9° C. After the deposition of Beds 4–6 the temperature rose again and the North Boreal species disappeared. This pattern of temperature change is summarized in text-fig. 13.

It is also possible to sketch the position of erosion base relative to the sea bed during the deposition of the *plenus* Subzone (text-fig. 13) on the assumption that an increase in mud content, or the presence of an erosion surface, indicate a fall in erosion base, and a decrease in mud content indicates a rise. There is no clear correlation between changes in the level of erosion base and changes in temperature.

The following distributional groups can be recognized in the fauna of the *plenus* Subzone:

(i) *Cold-water Group*. This includes forms characteristic of Bed 1 and the top of the *subglobosus* Zone which either do not occur higher in the *plenus* Subzone or else occur only very sporadically; they liked a temperature below equilibrium for aragonite. This group contains the macrofossils *Scapanorhynchus subulatus*, *Ctenothrissa* sp., *Plicatula inflata* (not in Bed 1), *Entolium orbiculare*, *Aequipecten beaveri*, *Neitheia quinquecostata*,



TEXT-FIG. 13. Temperature and turbulence changes in the *plenus* Subzone.

Lima globosa, *Lingula* sp., *Cretiscalpellum glabrum*, *Holaster trecensis*, *Discoidea cylindrica* (not in Bed 1), 'problematicum'; the benthonic foraminifera *Verneuilina polystropha*, *Tritaxia tricarinata*, *Dorothia gradata*, *Plectina ruthenica*, *Hagenowella advena*, *Pernerina* sp., *Nodosaria prismatica*, *Tristix excavatus* (not in Bed 1), *Gavelinella baltica*, *Pseudovalvulineria* sp.; and the planktonic foraminiferan *Thalmaninella deeckei*.

(ii) *Warm-water Group*. This includes forms which occur more or less abundantly in the beds above Bed 1 but which are rare or absent in that bed or in the *subglobosus* Zone in the area of standard succession and which liked a temperature at which aragonite

was not dissolved. It contains the macrofossils *Plicatula barroisi*, *Entolium membranaceum*, *Lina elongata*, '*Rhynchonella*' *lineolata carteri*, *Calliderma smithiae*, *Crateraster quinqueloba*, *Cidaris perornata*, *C. hirudo*, *Discoidea minima*, *Hemiaster uasutulus*; and the benthonic microfossils *Reophax* sp., *Textularia chapmani*, *T. cf. washitensis*, *Gaudryina* sp., *Siphogaudryina* sp., *Cibicides* cf. *turonica*, and *Anomalinoides globosa*, star plates and *Siphoniotyphlus tenuis*. Some of these forms were present or had relatives in shallow water in late *subglobosus* Zone times, while being absent or rarer in deep water during that period, e.g. *Discoidea minima* (related to *D. subuculus* of the *subglobosus* Zone), *Cidaris perornata*, *C. hirudo*, probably *Gaudryina* sp. and *Siphogaudryina* sp., *Cibicides* cf. *turonica*, and *Anomalinoides globosa*.

All of the macrofossils of this group were commoner in muddy beds than in pure ones which may partly be due to a liking for mud and partly due to slower deposition of the muddier beds. The situation at Bellignies suggests that *Quinqueloculina antiqua* and *Entolium membranaceum* liked mud and that *Siphoniotyphlus tenuis* and *Gaudryina* sp. probably disliked it.

(iii) *North Boreal Group*. This includes forms which are common in Beds 4–6 and which had relatives in the Central Russian Cenomanian of Arkhangelsky, viz. *Actinocamax plenus*, *Oxytoma seminudum*, and probably *Aequipecten arlesiensis*. These species probably liked cooler water than most of the warm-water group but not so cold as the cold-water group.

(iv) *Aragonitic Group*. Unlike the other groups the distribution of the aragonitic group (gastropods, scaphopods, aragonitic lamellibranchs, nautiloids, and ammonites) was controlled more by preservation than ecology. It is much to be hoped that other workers will look for groups comparable to these at other levels in the Chalk. It seems likely, for instance, that changes similar to the one at the base of Bed 2 will be found at the base of most bands in which aragonitic fossils are preserved (such as the Chalk Rock and Top Rock), and even at the base of any bands which are considerably harder than the beds beneath, suggesting the original presence of aragonite. To be useful such studies will have to be as quantitative as possible.

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A NEW BRITISH PERMIAN SPORE

by W. G. CHALONER and R. F. A. CLARKE

ABSTRACT. A new fossil miospore, *Vittatina hiltonensis* sp. nov., is described from the Hilton Plant Bed (Upper Permian), and compared with other Permian multistriate spores.

IN the course of a study of the spores from the Hilton Plant Bed (Zechstein, Upper Permian) of Westmorland, England, a new species has been found which may be assigned to the pollen genus *Vittatina* Luber. These spores were prepared by maceration of the shale of the Plant Bed with cold hydrofluoric acid, followed by concentration by flotation in bromoform. Single spore mounts in glycerine jelly were made between coverslips so that the spores could be examined under oil immersion from both sides; the spores illustrated here were mounted in this way.

Genus VITTATINA (? Luber 1940) Samoilovich 1953

There appears to be some uncertainty as to whether this genus was adequately validated by Luber in 1940; Potonié (1958, p. 90) was evidently unable to confirm publication of a valid type species at that date. We have been unable to trace the relevant work of Luber (see Samoilovich 1953, Potonié 1958), but accept Potonié's view that Luber may be regarded as author of the generic name. However, it remains uncertain whether the genus *Vittatina* was satisfactorily validated before Samoilovich's (1953) publication (undoubtedly valid) of the species *V. subsaccata*. The genus has since been used consistently by other authors (e.g. Potonié, Wilson) and we accordingly accept it in this sense.

Vittatina hiltonensis sp. nov.

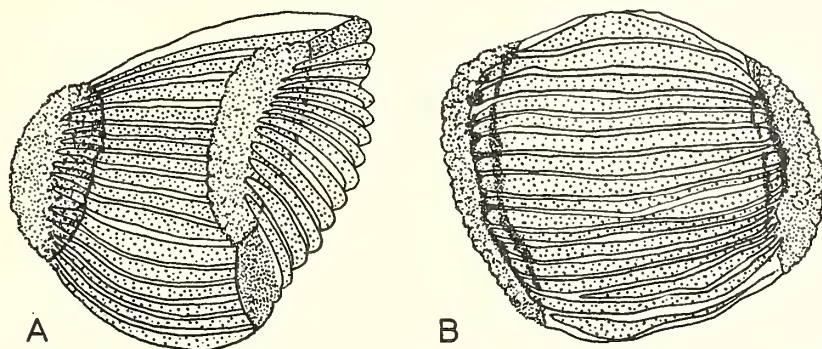
Plate 80, figs. 5–11; text-fig. 1A, B

Diagnosis. Spores bilateral as seen in polar view; long equatorial axis (Z in text-fig. 2), including the rudimentary sacci, 38–65 μ , mean of six specimens 55 μ ; short equatorial axis (W in text-fig. 2) 32–45 μ , mean of six specimens 39 μ . Entire proximal face of spore, excluding the rudimentary sacci, covered by thickened exinous elongations (ridges or muri) parallel with the long equatorial axis, and separated by relatively narrow furrows or striae, there being 15–18 ridges across the width of the proximal face. Each ridge typically has a maximum width of 2 μ , the furrows between being typically 0.5 μ wide. Exinous ridges semicircular in profile (seen on a folded edge), converging and narrowing towards the short sides of the spore as seen in polar view. They may be somewhat displaced, or twisted locally, or even die out; they do not appear to anastomose and are apparently restricted to the proximal face. In the two regions of convergence of the striations, exine locally cavate, producing features here referred to as rudimentary sacci, which show an obscure stippled pattern (seen at the right in Plate 80, fig. 7). Rudimentary sacci somewhat offset distally, so extending farther over the distal than the proximal surface (text-fig. 2, c and d). Rudimentary

sacci, seen in a flattened spore, $23\ \mu$ long (X, text-fig. 2) by $7\ \mu$ wide (Y, text-fig. 2), means of four measurements.

Holotype. Plate 80, figs. 5–7; Hilton Plant Bed, Hilton Beck, near Appleby, Westmorland, England. Geological Survey and Museum, London, slide number Mik (C) 514.

Discussion. In the fossil state the pollen has generally collapsed completely so that the proximal and distal faces of the grain are in contact. In all the specimens examined the



TEXT-FIG. 1, *Vittatina hiltonensis* sp. nov. $\times 1,000$ (drawn from photographs). A, Oblique polar view showing the form and extent of the thickened exinous bands and their relationship to the sacci. On the extreme left the striations are viewed distally through the saccus. The right-hand end shows the proximal striated surface folded over the smooth distal surface, and the extent of the thickened bands (see Plate 80, figs. 5–7). B, Polar view of an unfolded specimen with smaller sacci; the striations are again viewed through the distal surface (see Plate 80, figs. 10–11).

flattening is such that the spores are oriented with the polar axis more or less vertical. The whole grain may be somewhat curved so that the rudimentary sacci are frequently seen on edge (Plate 80, fig. 11, left-hand side) or are folded back over the grain (left-hand side of Plate 80, figs. 5–7) or seen in profile at the margin (Plate 80, fig. 6, right-hand side).

The sacci in the genus *Vittatina*, as illustrated by Samoilovich, are relatively very small, as compared with those of living *Pinus*, for example. Samoilovich refers to this state as 'subsaccate'. We describe these features as rudimentary sacci, without implying by this that we regard these features as representing phylogenetic precursors of true sacci. There seems to be no evidence either that this is the case, or (as is suggested by the term 'vestigial sacci' of some authors) that these structures are derived phylogenetically from an originally saccate state.

Comparison with other Permian Bilateral Multistriate Spores. The spores here assigned to *Vittatina hiltonensis* sp. nov. may be compared with the several genera of bisaccate multistriate spores which are such a characteristic feature of Permian assemblages in many areas. They show closest similarity to *Vittatina* Luber and *Protosacculina* Malavkina 1953. The type species of *Protosacculina*, *P. glabrescens* Malavkina, has relatively large sacci, equal to about half the bulk of the spore body, in contrast to the minute sacci shown by *Vittatina* as interpreted by Samoilovich. For this reason we assign our spore to *Vittatina*. Hart (1960) has taken a rather different interpretation of *Protosacculina*, and erects a new species of that genus which, he concedes, is closely similar (e.g. in its small sacci) to species included by other authors in *Vittatina*.

Our species, *Vittatina hiltonensis* sp. nov., is clearly similar to *V. subsaccata* Samoilovich, but differs from it in the longer sacci (our dimension X, text-fig. 2) and occasional anastomoses of the thickened bands in the latter species. Samoilovich's figure suggests anastomosis of the bands of thickening, but the possibility that this is an artefact produced by buckling of the proximal face cannot be ruled out. Our species can also be compared with *Protodiploxypinus bullaeformis* (? nom. nud.) Samoilovich 1953; this is illustrated but not described by Samoilovich, and although clearly similar to *Vittatina*, no comparison with that genus is made.

Spores very similar to *Vittatina hiltonensis* sp. nov. were reported by Wilson (1959) from the Flowerpot Formation (Middle Permian) of Oklahoma (cf. his '*Vittatina* sp.', pl. 1, fig. 15) and by Tschigouriaeva (1954) from the Russian Permian (cf. her fig. 14). *V. hiltonensis* sp. nov. could also be compared with *Welwitschiapites* Bolchovitina; the type species of this genus apparently lacked even rudimentary sacci, and is more *Ephedra*-like. Even in *W. alekhinii* Bolchovitina, which has minute saccus-like structures, these are very much smaller than in *Vittatina*. *Ephedripites* Bolchovitina is comparable in being multistriate but completely lacks evidence of even rudimentary saccus-like features. Some of the *Marsupipollenites* species of Balme and Hennelly 1956 (e.g. *M. fasciolatus* and *M. scutatus*, but not the type species) from the Australian Permian, are clearly similar to our species. Balme has already suggested (personal communication to W. G. C. Nov. 1957) that some of his multistriate species of *Marsupipollenites* might be better included in *Vittatina* rather than in the former genus. Alpern (1958) has described spores apparently similar to *V. hiltonensis* sp. nov., from the French Autunian, as *Aumancisporites*. Although he compares his spores to *Vittatina*, Alpern does not regard them as saccate, and apparently on this basis erects the new genus.

COMPARISON WITH *CLASSOPOLLIS BELLOYENSIS* POCKOCK AND JANSONIUS 1961

Pocock and Jansonius (1961) have recently revised the genus *Classopollis* and described a new Permian species, *C. belloyensis*. They record this species from the Permian

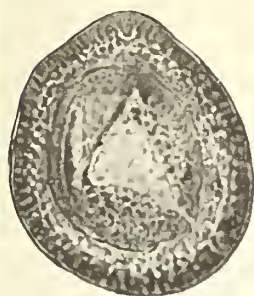
EXPLANATION OF PLATE 80

Magnification: figs. 3 and 4, $\times 2,000$. Remainder, $\times 1,000$.

Figs. 1–4, *Classopollis torosus* (Reissinger) Balme, Rhaetic. 1, Polar view, showing triangular proximal aperture, thin sub-equatorial zone encircling it, and wall structure (Henfield borehole, Sussex). 2, Equatorial view of another specimen; 3, the same, showing the thickened equatorial zone in profile; 4, the same at higher focal plane, showing equatorial striations at centre (Foxholes No. 2 borehole, Owthorpe, Nottinghamshire).

Figs. 5–11, *Vittatina hiltonensis* sp. nov. from the Hilton Plant Bed, Upper Permian. 5–7, Oblique polar view of distal face, in successively higher focal planes. The striations are on the proximal face, and are seen through the smooth distal face. Rudimentary saccus at right (seen most clearly at 7). At left, the proximal face is folded over the distal, and shows the extent of the thickened bands on the proximal side of the saccus. 8–9, Another specimen with rather less prominent rudimentary sacci; the higher focal plane is at 8 (the proximal striations are seen through the distal face). 10–11, Another specimen in polar view, in two focal planes. Note irregularities in the continuity of the thickened bands. The rudimentary saccus is seen in sharp focus at right, in 11.

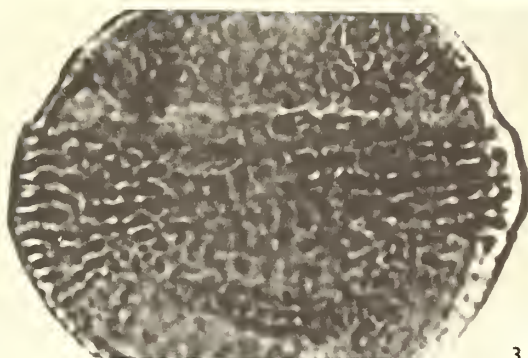
All preparations in the Geological Survey and Museum, London; fig. 1: Mik(C) 314; figs. 2–4: Mik(J) 304; figs. 5–7: Mik(C) 514; figs. 8–9: Mik(C) 512; figs. 10–11: Mik(C) 513.



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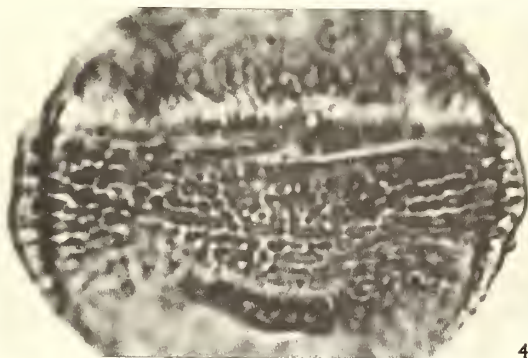
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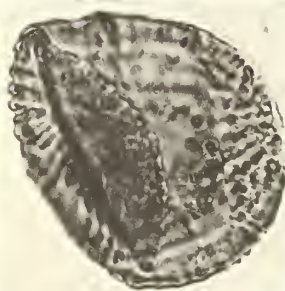
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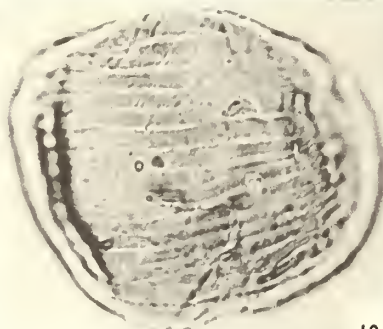
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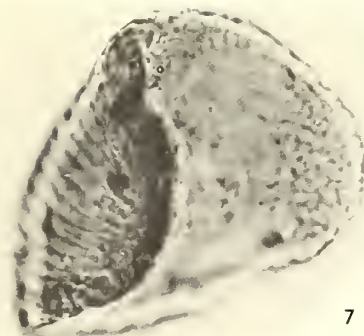
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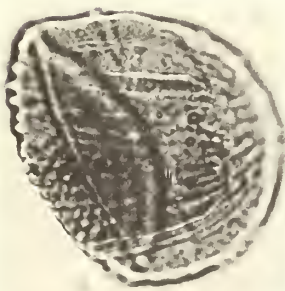
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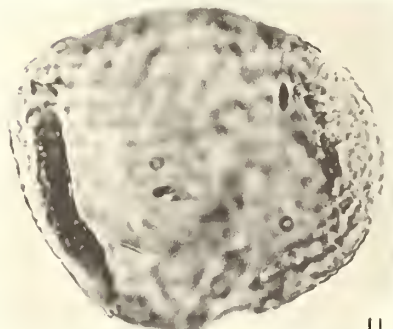
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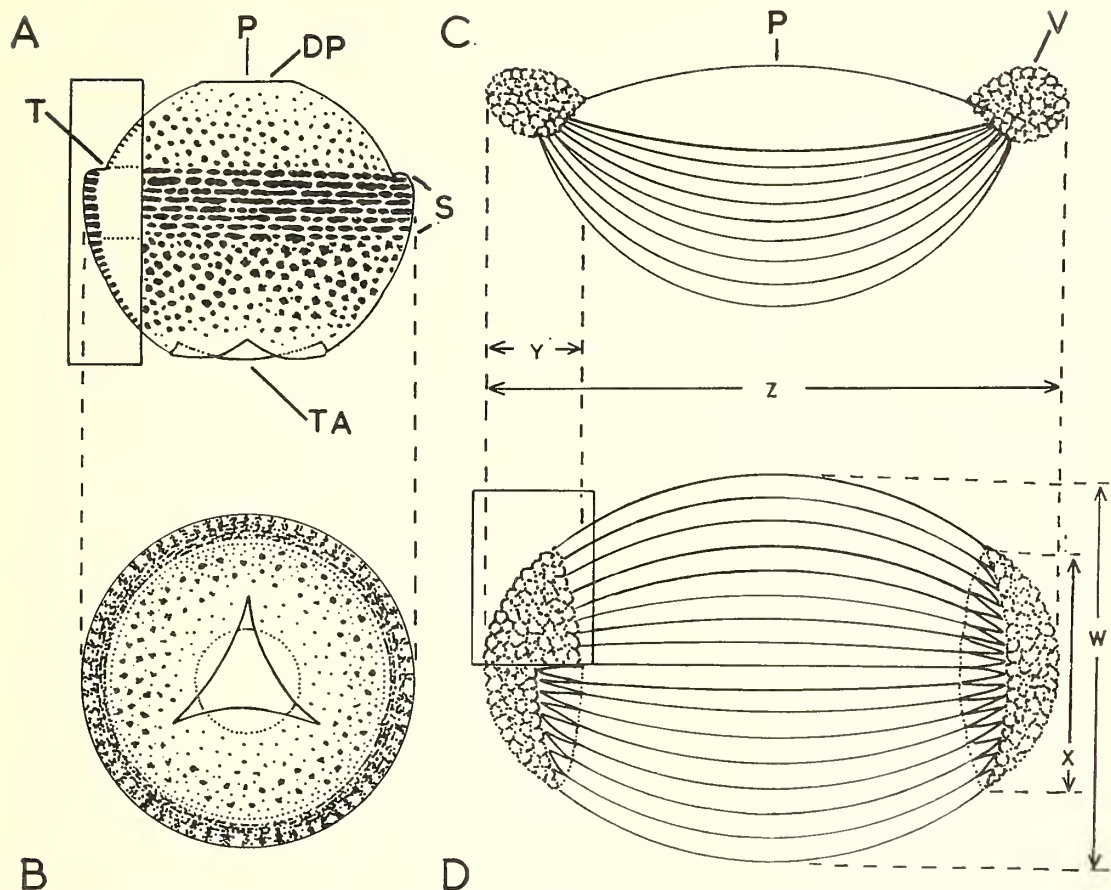
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11

Classopollis

Vittatina



TEXT-FIG. 2. Diagrammatic reconstructions of *Classopollis torosus* (Reissinger) Balme (A, B) and *Vittatina hiltonensis* sp. nov. (C, D), $\times 1,000$. Above, equatorial views; below, polar views. The rectangle in A shows the spore wall in section; that in D shows the distal view of the rudimentary saccus, the remainder of the drawing showing the proximal view. P, polar axis; D.P., distal pore; S, equatorial striations; T, thin-walled subequatorial zone; T.A., triradiate aperture (proximal); V, rudimentary saccus; W, X, Y, Z, dimensions referred to in the text.

of both Canada and the Hilton Plant Bed, Westmorland. While we accept the general interpretation of *Classopollis* proposed by those authors on the basis of the type species, we believe that their Permian spore lacks sufficient diagnostic characters of that genus to be included in it. A comparison of Pocock and Jansonius's figures of *Classopollis belloyensis* with *Vittatina hiltonensis* suggests the possibility that their species might represent a spore of comparable organization to *Vittatina* rather than *Classopollis*. If this were so, their figure would correspond with a polar view of a *Vittatina*-like subsaccate striate pollen grain, rather than an equatorial view of a *Classopollis*. The features which

Pocock and Jansonius interpret as an equatorial girdle seen in profile might then correspond with the rudimentary sacci of a *Vittatina*. This would be equivalent to equating our text-fig. 2A with text-fig. 2D. Plate 80, figs. 1 and 2, show Rhaetic specimens of *Classopollis torosus* (Reissinger) Balme (= *C. classoides* sensu Pocock and Jansonius) in polar and equatorial view, and Plate 80, figs. 3 and 4, part of the equatorially thickened and striate region at higher magnification (these two views are shown diagrammatically in text-fig. 2A and B). It is as such a view of *Classopollis* that Pocock and Jansonius interpret their *C. belloyensis* (plate 1, fig. 10). As those authors do not show their spore in polar view, they offer little convincing evidence to support the presence of a circular distal pore, a proximal triradiate feature, or completely encircling equatorial striations, all of which are characteristic of *Classopollis* on their own interpretation. Further, their plate 1, fig. 11, shows striations extending beyond the region of the supposed equatorial girdle, so inviting comparison rather with our text-fig. 2D than with our text-fig. 2A (i.e. a *Vittatina*-like organization rather than a *Classopollis*-like one). For these reasons it seems premature to assign *Classopollis belloyensis* to this genus. If *C. belloyensis* is excluded from the genus *Classopollis*, the genus in this restricted sense then ranges from the Rhaetic to the Cretaceous. Tertiary records are uncertain and may well represent derived Mesozoic specimens. *Vittatina*, on the other hand, has been recorded with certainty from the Permian of Russia, the United States, Australia, and Britain.

Acknowledgement. We would like to express our thanks to the Department of Scientific and Industrial Research from which one of us (R. F. A. C.) has been in receipt of a grant during the course of this work.

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BRACHIOPOD LIFE ASSEMBLAGES FROM THE MARLSTONE ROCK-BED OF LEICESTERSHIRE

by A. HALLAM

ABSTRACT. Clusters of brachiopods in the Marlstone Rock-bed of Leicestershire are interpreted as life assemblages. It is tentatively suggested that at least three successive annual broods may be present. The colonies came to a sudden end, probably through burial by sediment.

THE Marlstone Rock-bed of the Middle Lias is well known for the richness and variety of its fauna, most notably brachiopods (Ager 1956). A striking feature of the Marlstone in the Midlands is the common occurrence of brachiopods in discrete and often tightly packed clusters of beautifully preserved shells. The present study of some of these clusters in Leicestershire follows on an earlier tentative inference (Hallam 1955) that they represent true colonial associations.

The Marlstone in the Midlands consists predominantly of oolitic ironstone, more specifically a calcitic, sideritic chamosite oolite (Whitehead *et al.* 1952) but in parts of Leicestershire and south Lincolnshire the lower few feet are made up of calcareous sandstone. It is generally accepted that the oolite was deposited in conditions of strong current action in a warm, shallow sea enriched in iron.

Fossils are distributed in the ironstone as follows:

(1) *Brachiopod clusters.* These consist of small clusters of closely packed brachiopods exhibiting wide size variation and random orientation. Disarticulation is slight and almost all the shells have their interiors filled with coarsely crystalline calcite. Signs of disturbance by currents are slight. Details of the location of some of these clusters or 'nests' in Leicestershire are given in Hallam (1955). In the rail cutting near Tilton is a 1-foot band composed of brachiopods (band A) about $2\frac{1}{2}$ feet above the base of the Marlstone. This has been formed by the lateral coalescence of clusters of *Tetrahynchia tetrahedra* and *Lobothyris punctata* (J. Sowerby). These clusters form the subject of the next two sections.

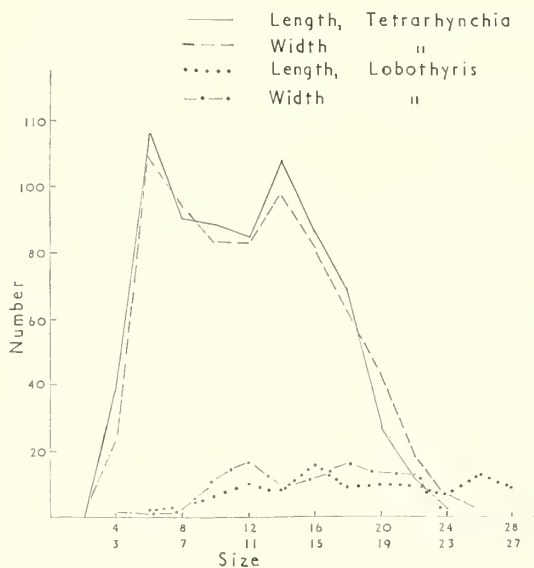
(2) *Disturbed shell bands.* These consist mainly of pelecypods, brachiopods, and belemnites. The first two groups are mostly disarticulated, especially the pelecypods. The interiors of articulated brachiopod shells are often filled with sediment; broken and crushed shells are common. Separated valves are usually oriented parallel to the bedding, e.g. band B near Tilton (Hallam 1955). The bands are usually less than an inch thick and are rarely traceable for more than a few hundred feet. Brachiopod clusters may grade into bands.

(3) *Scattered fossils.* Crinoids, an important component of the rock, are always disarticulated into small ossicles. These ossicles commonly occur as lenses and may mark out current bedding. A wide variety of other fossils occur as scattered shells.

DESCRIPTION OF THE BRACHIOPOD CLUSTERS

Samples of several brachiopod clusters, containing the species *Tetrahynchia tetrahedra* and *Lobothyris punctata* (J. Sowerby), were collected from two quarries in the neigh-

bourhood of Branston in north-east Leicestershire (N.G. 814295 and 806288), a particularly favourable locality. Clusters are commonest near the base of the ironstone but they are not confined to any one level. They tend to be subspherical or ellipsoidal in shape, with the long axis parallel to the bedding. They range in size up to 50 cm. in width and 15 cm. in height. The shells are almost all infilled with crystalline calcite and separate valves are rare. Distortion in shape is fairly common but fracture rare. No variation in shell size is readily discernible in different parts of the clusters. The clusters



Text-fig. 1. Sample 1 from Branston.



TEXT-FIG. 2. Sample 2 from Branston.

TEXT-FIGS. 1-6. Length and width frequency diagrams of samples of brachiopod clusters from Branston, Leicestershire. The key is given in text-fig. 1.

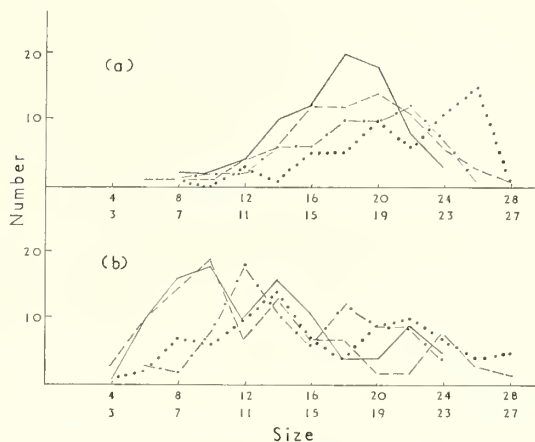
are isolated in much less fossiliferous rock containing scattered brachiopods and belemnites, sometimes concentrated into thin bands. The lithology throughout seems uniform. As the rock matrix is hard it was found impossible to collect complete clusters—indeed, a cluster is only visible if part has been removed by quarrying. The assumption is made that the samples collected are representative of complete clusters.

An attempt was made to extract all the brachiopods from the rock samples. This was effected by thorough mechanical breakdown, which is facilitated a little by immersing material in hot, concentrated evaporating solutions of Na_2SO_4 (no conventional chemical technique can be applied as the shells are composed of CaCO_3). Because of the hardness of the matrix some of the larger specimens were fractured during the process but with care the fragments could be fitted together, so that the number actually lost is very small. Particular care was taken to collect small specimens and the number missed below a length of 4 mm. is probably only small so that if anything there is a slight bias in collecting towards small size. In this way over 4,000 brachiopods were obtained.

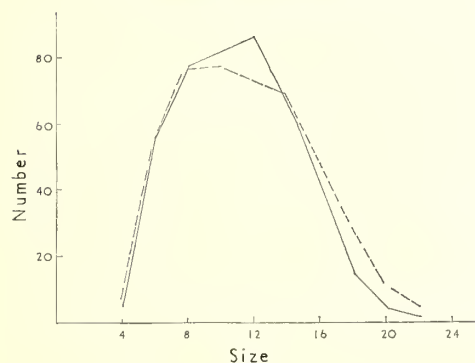
Size-frequency graphs of samples from seven different nests were plotted and are reproduced in text-figs. 1 to 6. Both length and width were measured and plotted to



TEXT-FIG. 3. Sample 3 from Branston.
For key see text-fig. 1.



TEXT-FIG. 4. (a) Sample 4 and (b) sample 5 from
Branston.



TEXT-FIG. 5. Sample 6 from Branston. For
key see text-fig. 1.



TEXT-FIG. 6. Sample 7 from Branston.

give a reliable index of size. It will be seen from the figures that the shape of the size-frequency curves is closely similar for both measurements.

Measurement was made in millimetres but in order to obtain a clearer picture of the broad features of the size frequency distributions and reduce the risk of incorporating accidental variations, the measurements were grouped together in pairs of millimetres in two ways, 3-4, 5-6, &c., and 4-5, 6-7, &c. Both sets give closely similar curves, so only one is illustrated.

It will be observed that in the Branston clusters *T. tetrahedra* is much commoner than *L. punctata*, which may be completely absent. There is no danger of confusing the two species even with the smallest specimens. The wide size range and the high percentage of small specimens in the samples is striking. Considering for the moment only *Tetrarhynchia*, the curves of samples 1, 2, 6, and 7 are slightly left-skewed and 3 and 4 roughly symmetrical. Those of samples 1 and 3 are clearly bimodal, with peaks at $\frac{5}{6}$, $\frac{13}{14}$, $\frac{7}{8}$, and $\frac{15}{16}$ respectively. The results for samples 4 and 5 are less reliable because of the much smaller number of specimens. They came from volumes of rock similar to the others but the percentage of small specimens is much lower.

An interesting feature is the rarity of specimens of length less than 5 mm.; $5\frac{1}{2}$ per cent. is the maximum in any sample for the $\frac{3}{4}$ mm. grade. No specimens of *Tetrarhynchia* of less than 3 mm. and *Lobothyris* of less than 5 mm. were discovered. This can be attributed to collection failure only to a limited degree, since the rock matrix was carefully scrutinized for such material.

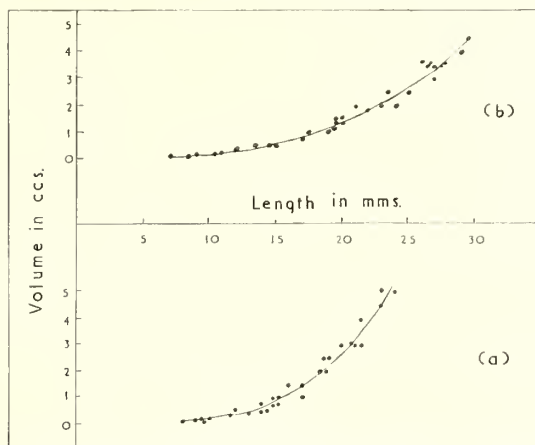
INTERPRETATION

There is strong evidence in favour of the clusters being genuine life assemblages (in the sense of Boucot 1953).

- (1) There are few signs of physical disturbance of the shells.
- (2) There is a wide size range in the shells, not suggestive of sorting by currents.
- (3) The clusters are not random samples of the Marlstone fauna. It is highly exceptional for them to contain any fossils besides brachiopods.
- (4) It is inherently improbable that clusters of brachiopods would be swept together by bottom currents. The evidence of the disturbed shell bands suggests rather the reverse.
- (5) In three cases out of four, there is a pronounced lack of coincidence in the shape of the size-frequency curves for *Tetrarhynchia* and *Lobothyris* in the same cluster (text-figs. 1, 2, and 4). There is no reason to expect similarity if the fossils represent original living associations, whereas if the shells had been sorted to any extent after death they would tend to be grouped according to size regardless of biological differences. Variation in volume is the most important factor controlling the possible distribution of shells by currents (the more subtle factors of weight and shape, which are not readily measurable, may be disregarded in a rough analysis). Therefore, to test the supposition that the differences in the curves reflect genuine differences of volume, a volume/length curve was plotted for a number of specimens of *Tetrarhynchia* and *Lobothyris* from the samples (text-fig. 7). The most pronounced differences occur in sample 1. The two peaks in the *Tetrarhynchia* curve correspond to volumes of about 0.10 and 0.50 c.c., while the *Lobothyris* curve has a low mode at 0.65 c.c. While 57 per cent. of the *Tetrarhynchia* specimens have a volume less than 0.35 c.c. only 29 per cent. of the *Lobothyris* specimens fall in this range. The shapes of the two curves differ markedly also in sample 2, the mode for *Tetrarhynchia* being at about 0.10 c.c. and that for *Lobothyris* at about 0.25 c.c. Data for the much smaller samples 4 and 5 are naturally less reliable but at least in the case of sample 4 there appears to be an appreciable difference. Not only do the shapes of the curves differ but the mode for *Tetrarhynchia* (c. 1.7 c.c.) is less than that for *Lobothyris* (c. 2.8 c.c.). There is therefore justification for maintaining that differences in the shapes of the curves reflect genuine differences in the size distributions of *Tetrarhynchia* and *Lobothyris* from the same samples.

It follows from acceptance of the clusters as life assemblages that *Tetrarhynchia* and *Lobothyris* lived in intimate association.

The general shapes of the size-frequency curves may now be considered further. Boucot (1953) suggested that life and death assemblages may be distinguishable on the basis of size-frequency curves, the former tending to have strongly left-skewed distributions with the right-hand portion concave upwards, the latter having normal or gaussian distributions. The curves in text-figs. 1 to 6 do not correspond closely to either pattern. The reason is not far to seek. It is apparent from the work of Olson (1957) that fossil assemblages may approximate to theoretical predictions only if the factor of annual



TEXT-FIG. 7. Volume/length relationships in samples of (a) *Tetrarhynchia* and (b) *Lobothyris*.

broods and population fluctuations can be rendered negligible. But this is only possible if specimens are collected from beds deposited in a space of time considerably greater than a few years, in which case the chance of a genuine life assemblage being preserved and accurately sampled is slight. This is a serious defect of the technique Boucot proposed and one must endorse Olson's view that other criteria should be sought, as in the present work.

If, then, it may be accepted that the irregular character of the curves in text-figs. 1 to 6 is due to the influence of successive broods, there exists the possibility of recognizing annual groups in the populations. The only relevant published work on living brachiopods known to the author is that of Percival (1944). However, Dr. M. J. S. Rudwick has recently made a similar study of living brachiopod populations in New Zealand and obtained results much different from those of Percival. He has kindly offered the following remarks:

'The size distribution of my samples of *Terebratella inconspicua* is markedly two-peaked, in striking contrast to Percival's sample, which shows no trace of a peak of large shells. At all the localities I have seen, living populations are conspicuous for their high proportion of large and mature individuals. Percival's sample was, I believe, highly abnormal in this respect, probably because it was collected from such a small area of stones. Owing to the very patchy distribution of the shells, 2.3 square decimetres

is far too small an area to ensure a representative sample of the population. I can only infer that the small stones from which his sample came happened to be occupied by a very dense patch of shells from the most recent spatfall, and did not include any of the patches of the large and mature individuals that comprise the bulk of the population. My samples were collected from areas of boulder-surface more than ten times Percival's area, yet even so there are individual differences between them that suggest that even they are not accurately representative, though much more so than Percival's.'

Dr. Rudwick believes that the troughs between the two peaks in his samples do not necessarily represent the interval between successive broods but could be due to the local failure of intervening broods.

In the case of *Tetrahynchia*, the two peaks in samples 1 and 3 are probably reliable in view of the large number of specimens involved and the technique applied of grouping measurements in pairs of mms. It is interesting to note that the spacings of the peaks, $\frac{5}{8}$ and $\frac{13}{14}$ mm. in sample 1 and $\frac{7}{8}$ and $\frac{15}{16}$ mm. in sample 3, are identical, suggesting that they may reflect separate broods of slightly different ages. The uniformity and small amount of the spacing between the peaks suggests that we may indeed be dealing with successive broods. Bearing this in mind, the main features of the other large sample (2) could be accounted for by the presence of large first- and second-year broods with modes at $\frac{7}{8}$ and $\frac{15}{16}$, as in sample 3. The slight shallowing of the right-hand end of the curves in samples 1, 2, 3, 6, and 7 could be due to the presence of a few specimens of a third-year age group. Recognition of such a group is bound to be more difficult both because of the relatively small number of forms which would survive to the third year and because of a slowing down of growth.

If the assumption that annual groups are normally distributed is correct (Olson 1957) the possibility exists of separating different broods in a given sample. Unfortunately, one would have to work from the steep left-hand part of the curve and this may be the least reliable. In view of this and the number of uncontrollable variables involved, statistical analysis would be likely to give valid results only with a far greater number of samples. The evidence seems good enough, however, to allow the tentative suggestion that the clusters sampled are composed of at least three successive annual broods, but in view of Dr. Rudwick's remarks, confirmation will have to await the results of a much greater quantity of work on living brachiopod populations.

The absence of specimens of length less than 3 mm. and 5 mm. in *Tetrahynchia* and *Lobothyris* respectively may be due to predation. It is questionable whether the rarity of small specimens in sample 4 is due to their selective removal by currents.

Recognition of the clusters as colonial associations poses an interesting problem. It is apparent from the work of Menard and Boucot (1951) that brachiopod shells filled with water are moved by currents much more readily than coarse sand. The critical velocity for effecting such movement is very low, no greater indeed than that of natural currents operating at a depth of more than 1,000 fathoms in the Pacific Ocean. But the sedimentary evidence for the Marlstone in general strongly suggests the operation of powerful bottom currents.

Presumably the colonies grew in periods of comparative quiescence. Yet as even weak currents could have sufficed to disperse shells after the pedicles had decayed, one is forced to the conclusion that the living colonies were killed by a sudden change of environment and preserved within the sediment as discrete clusters. Bearing in mind

the nature of the Marlstone environment as deduced from the sedimentary evidence, it is quite probable that they were overwhelmed by the movement of sediment on the sea bottom. If growth were allowed to continue for long enough, the clusters would tend to spread over the sea floor and eventually coalesce. This appears to have happened in at least one case, that of band A near Tilton, which was mentioned earlier.

The writer is indebted to Drs. G. Y. Craig and M. J. S. Rudwick for valuable comments and criticisms.

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Manuscript received 20 April 1961

THE PALAEOONTOLOGICAL ASSOCIATION

Extracts from the Annual Report of the Council for 1960-1

MEMBERSHIP. On 31 December 1960 there were 860 members (499 Ordinary and 361 Institutional), a net increase of 136 members. The rate of increase in membership accelerated abruptly after the distribution of the brochure advertising *Palaentology* which was financed by a generous grant from the Nuffield Foundation.

FINANCE. The Balance Sheet and Accounts for 1960 are given below. 1960 has been a critical year in the finances of the Association. At the end of 1959 Council decided to double the publication rate of *Palaentology* and to increase the annual subscription, but the latter could not come into effect until 1961. In 1960, therefore, expenditure was doubled although income from subscriptions remained substantially the same as in previous years. In consequence it has been necessary to lean heavily on the generosity of the oil companies making donations to the Association.

Two other sources of funds have allowed the Association to complete the year without running into a deficit. The income from Special Donations made towards the cost of particular papers has greatly increased, and income from sales of back parts has more than doubled. The latter increase is in no small measure due to the grant from the Nuffield Foundation, and the effect of the promotion scheme is continuing. The Association can therefore face 1961-2 in the confidence that it can continue to finance the regular publication of four parts of *Palaentology* per year.

'PALAEOONTOLOGY.' Volume 2, part 2 (for 1959), and the four parts of Volume 3 (for 1960) were published during 1960-1. They contained forty-seven papers. It remains the policy of the Association to devote the major part of its income to publishing *Palaentology*.

MEETINGS. Six meetings were arranged during 1960-1. The Association is grateful to the Council of the Geological Society of London; the Director of the Geological Survey and Museum; Dr. F. E. Eames (British Petroleum Company); Mr. Ellis Thirkettle (London School of Printing and Graphic Arts); and Prof. T. N. George (University of Glasgow) for generously granting facilities for meetings, and to the Local Secretaries for their efficient services.

- a. The third Annual General Meeting was held in the Rooms of the Geological Society of London, Burlington House, W. 1, on Wednesday, 9 March 1960, at 5.0 p.m. The Annual Report of the Council for 1959 was adopted, and the Council for 1960-1 elected. Dr. R. G. S. Hudson delivered the Third Annual Address on 'Tethyan Faunas'.
- b. A Demonstration Meeting was held in the British Petroleum Research Centre, Sunbury-on-Thames, Middlesex, on Saturday, 7 May 1960, to inspect the geological laboratories and examine palaentological exhibits arranged by members of the Research Centre.
- c. A Visit to the London School of Printing and Graphic Arts, London, E.C. 1, took place on Wednesday, 12 October 1960, to study printing processes.
- d. A Lecture by Prof. Dorothy Hill (University of Queensland) on 'The fine structure of the coral skeleton and its application in classification' was delivered in the Rooms of the Geological Society of London, on Wednesday, 9 November 1960.
- e. A Discussion Meeting was held in the Department of Geology, The University, Glasgow, on 16/17 December 1960. The subject was 'Palaeo-ecology'. About 75 persons attended. Twelve papers were read during two sessions, and there were 26 exhibits. A dinner was held in the University College Club on 16 December. Dr. W. W. Bishop was the Local Secretary.
- f. A Discussion and Demonstration Meeting on 'Bibliographic Aids in Palaentology' was held in the Geological Survey and Museum, London, on Wednesday, 18 January 1961. The organizer was Prof. P. C. Sylvester-Bradley, and the Local Secretary Mr. J. D. D. Smith.

COUNCIL. In accordance with Rule 3 of the Constitution, as amended on 20 January 1960, an Assistant Secretary, Assistant Treasurer, and two extra Editors were appointed as additional Officers to cope

with the increasing volume of the Association's work. The following were elected members of the Council of the Association for 1960-1 at the Annual General Meeting on 9 March 1960: *President*: Prof. O. M. B. Bulman, *Vice-Presidents*: Prof. T. N. George, Dr. R. G. S. Hudson, *Treasurer*: Prof. P. C. Sylvester-Bradley, *Assistant Treasurer*: Dr. T. D. Ford, *Secretary*: Dr. Gwyn Thomas, *Assistant Secretary*: Dr. C. H. Holland, *Editors*: Dr. W. H. C. Ramsbottom, Mr. N. F. Hughes, Dr. W. S. McKerrow. *Other members*: Dr. D. V. Ager, Dr. F. T. Banner, Mr. M. A. Calver, Dr. W. G. Chaloner, Dr. A. J. Charig, Dr. L. R. Cox, Dr. R. H. Cummings, Dr. J. C. Harper, Prof. F. Hodson, Prof. L. R. Moore, Dr. Dorothy H. Rayner, Mr. J. D. D. Smith, Dr. I. Strachan, Dr. C. J. Stubblefield.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1960

BALANCE SHEET

Liabilities

	£	s.	d.	£	s.	d.
Publications Reserve Account						
Balance as per Annexed Account				2,781	5	5
Amounts Received in Advance:						
Subscriptions for 1961	920	0	9			
Special donation towards cost of <i>Palaeontology</i> , Vol. 4	44	0	0			
				964	0	9
Provision for cost of publication of <i>Palaeontology</i> , Vol. 3 as per						
Income and Expenditure Account	4,158	17	8			
Less Expenditure incurred to 31 December 1960	2,149	16	2			
				2,009	1	6
Sundry Creditors				18	10	1
				<u>£5,772</u>	<u>17</u>	<u>9</u>

Assets

Investments at cost—5% Defence Bonds				3,000	0	0
Sundry Debtors:						
Authors for reprints	137	16	8			
Nuffield Foundation (special grant)	231	9	1			
Donations (promised, not yet received)	650	0	0			
				1,019	5	9
Cash at Bank—Deposit Account	851	19	0			
Current Account	901	13	0			
				1,753	12	0
				<u>£5,772</u>	<u>17</u>	<u>9</u>

Report of the Auditors to the Members of the Palaeontological Association. We have examined the above Balance Sheet and annexed Income and Expenditure Account which in our opinion give respectively a true and fair view of the state of the Association's affairs as at 31 December 1960 and of its income and expenditure for the year ended on that date.

BAKER BROS. HALFORD & CO.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT

Expenditure

	£	s.	d.	£	s.	d.
To Provision for cost of publication of						
<i>Palaeontology</i> , Vol. 3, Part 1	903	17	8			
Part 2	905	0	0			
Part 3	835	0	0			
Part 4	1,515	0	0			
				4,158	17	8
Administrative Expenses:						
Postage and stationery	111	19	11			
Insurance	3	2	6			
Audit fee	5	5	0			
Miscellaneous	28	10	2			
Cost of distribution of publications	94	8	6			
				243	6	1
Excess of Income over Expenditure for the year transferred to Publications Reserve Account				372	11	3
				<u>£4,774</u>	<u>15</u>	<u>0</u>

	£	s.	d.	£	s.	d.
<i>Income</i>						
By Subscriptions for 1960				1,520	3	5
Subscriptions for previous years				58	16	0
Sales of publications				669	5	10
Authors for reprints of <i>Palaeontology</i> , Vol. 2	287	3	7			
Less expenses incurred on this Volume in excess of provision at 31 December 1959	153	6	2			
				133	17	5
Receipts from advertising				24	0	3
Interest received— 5% Defence Bonds	135	1	7			
Bank Deposit Account	47	10	6			
				182	12	1
Special Donations: Royal Society, Iraq Petroleum Co. Ltd., Carnegie Trust, R. Casey (Shell International Research)				1,061	0	0
General Donations: Attock Oil Co. Ltd., British Petroleum Co. Ltd., Burmah Oil Co. Ltd., Iraq Petroleum Co. Ltd., Kuwait Oil Co. Ltd., Texaco Inc., Ultramar Co. Ltd.				1,125	0	0
				<u>£4,774</u>	<u>15</u>	<u>0</u>

PUBLICATIONS RESERVE ACCOUNT

	£	s.	d.
Balance per Balance Sheet.	2,781	5	5
	<u>£2,781</u>	<u>5</u>	<u>5</u>
Balance at 31 December 1959	2,000	0	0
Transfer of Excess of Income over Expenditure:			
Year ended 31 December 1959	408	14	2
Year ended 31 December 1960	372	11	3
	<u>781</u>	<u>5</u>	<u>5</u>
	<u>£2,781</u>	<u>5</u>	<u>5</u>

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